THE EVOLUTIONARY SIGNIFICANCE OF LIFE HISTORY DIVERGENCE AMONG BROOK TROUT, *Salvelinus fontinalis*, POPULATIONS

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by

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ABSTRACT

I combined field studies, laboratory experiments, and empirically-based model simulations to study life history variation among seven populations of brook trout, Salvelinus fontinalis, on Cape Race, Newfoundland. My objectives were to describe population variation in life history on a small geographical scale, to identify the environmental factor(s) responsible for effecting inter- and intra-population life history differences, and to assess the evolutionary significance of the observed variation through empirical tests of life history theory.

There were significant population differences in life history. Growth rate differed 2-fold between the most divergent populations. Among populations, the slowest growing females 1) matured at an early median age at the smallest mean size relative to the fastest growing females (3 yr, 99.8 mm versus 5 yr, 164.1 mm), 2) produced the largest eggs (4.43 mm vs. 4.01 mm), 3) had the highest size-specific fecundity, and 4) allocated proportionately the most body tissue to gonads.

Estimates of offspring and maternal fitness depended on egg size, the trade-off between egg size and egg number, and juvenile food abundance. Egg diameter was positively correlated with embryonic and juvenile size but had no

significant effect on embryonic survival or developmental time in laboratory reared fish. Juvenile survival was linearly related to egg size throughout the first 50 days of exogenous feeding at high and low food levels. Reduced food increased mortality significantly among the smallest eggs but not among the largest eggs. Empirically-based simulations 1) supported the hypothesis that environments with low food abundance select for increased offspring size, and 2) indicated that unpredictable, temporally heterogenous environments favour constant, rather than variable, investment in offspring size.

There are costs of present reproduction to future survival in brook trout and these costs vary among populations. For a given reproductive effort, reductions in both size at maturity and resource abundance appear to increase reproductive costs. These costs appear to have a physiological basis: allocation of lipids to gonad production and their subsequent loss during autumnal reproduction decreases the fat stores available to meet energetic demands during winter. Reproductive costs and reproductive effort are related in a concave-shaped function that can account for the evolution of alternative expenditures of reproductive effort in brook trout.

Population differences in brook trout life history can be explained as adaptive responses to differences in growth rate effected primarily by differences in food abundance.

Reduced growth results in high reproductive investment near the physiologically minimum size at maturity. Individual life history traits appear to be consequences of the survival and fecundity costs associated with differential size- and age-specific reproductive investment.

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Chapter One

INTRODUCTION

Life history theory attempts to predict the probability distribution of reproductive strategies (genetically based patterns of phenotypic trait covariation) that will evolve in different environments. Within this framework, the thesis addresses several aspects of life history theory. For example, which environments favour individuals that produce many, small offspring over individuals that produce few, large offspring (Smith and Fretwell, 1974; Sibly and Calow, 1983). Which environments favour the production of several broods over an individual's lifetime rather than the production of a single brood in one, suicidal, reproductive bout (Cole, 1954; Gadgil and Bossert, 1970; Schaffer, 1974a,b; Bell, 1980). Implicitly, this issue addresses the question of how much effort individuals should invest in reproduction at any one time given that effort expended during present reproduction may be done so at a cost to future reproduction (Williams, 1966; Charlesworth and León, 1976; Law, 1979a,b, Michod, 1979). Reproductive effort is the proportion of total energy that an individual devotes to the behavioural and physiological elements of reproduction (Hirshfield and Tinkle, 1975). It includes maturation, mate

choice, competition for mates, establishment and defense of breeding sites, and parental care.

1.1 Review of the Theory

Reproductive strategies reflect the ways in which organisms vary their age-specific expenditures of reproductive effort in response to environmentally-induced changes in age-specific mortality. The most divergent age-specific expenditures of reproductive effort are between iteroparous and semelparous reproductive strategies (Cole, 1954; Gadgil and Bossert, 1970; Schaffer, 1974a,b). The magnitude of these age-specific expenditures depends primarily on their relative influence on offspring and parental survival (Cole, 1954; Gadgil and Bossert, 1970; Schaffer, 1974a,b; Hirshfield and Tinkle, 1975; Pianka and Parker, 1975; Schaffer and Rosenzweig, 1977). For example, a postponement of present reproduction may be favoured by selection if the benefits (e.g. increased body size or learning) that postponement confers upon future reproduction more than compensates for the present loss of offspring and the probability of future adult mortality (Charlesworth, 1980).

Fisher (1930) was the first to recognize the selective importance of how organisms partition energy into growth, reproduction and maintenance. He stated that:

> "It would be instructive to know not only by what physiological mechanism a just apportionment is made between the nutriment devoted to the gonads and that devoted to the rest of the parental organism, but also what circumstances in the life-history and environment would render profitable the diversion of a greater or lesser share of the available resources towards reproduction."
>
> - R.A. Fisher (1930: 47)

To understand how these age-specific "apportionments" evolved, Fisher (1930) posited that selection must be related to an individual's age-specific expectation of future offspring. He defined this expectation as reproductive value (RV). That is, the reproductive effort expended by an organism at any age will be under natural selection, will maximize fitness, and will depend, in part, on the probability of future reproduction. Fisher (1930:39) considered r, the intrinsic rate of increase, to be the most appropriate measure of fitness - a view supported by current life history theorists (Charlesworth, 1980). Life history strategies that maximize fitness are evolutionarily stable (i.e., a rare gene introduced into a population will be eliminated if its carriers have a phenotype different from the population mean (Maynard Smith, 1972; Charlesworth, 1980)).

Following Fisher's reasoning, reproductive effort will depend primarily on age. Evolutionarily stable ages at maturity are based on the maximization of 1) the rate at which an individual's offspring are introduced into the gene

pool and 2) the number of offspring produced in a lifetime (Charlesworth, 1980). Both of these are influenced directly by growth rate in many organisms (Stearns and Koella, 1986). Once the physiologically minimum reproductive size is attained, an individual's reproductive strategy will be based on the relative benefits of reproducing at present (maximizing the rate of gene input but possibly at some cost to future fecundity and/or survival) or of delaying reproduction (maximizing fecundity but at the cost of mortality in postponing reproduction to that later time). If individuals reproduce at a size near the physiological minimum, then either (1) the costs to survival and to the rate of gene input in the population of postponing reproduction outweigh the benefits of increased size and higher fecundity, or (2) there are negligible survival and fecundity costs to reproduction such that individuals reproduce as early in life and as frequently as possible to maximize both rate of gene input and fecundity.

The logical necessity of reproductive costs is based on the concept that organisms are energetically constrained systems (Calow, 1979). For example, the allocation of energy to gonads cannot be made without some somatic cost in terms of the energy allocated for growth and body maintenance (unless the organism is able to produce surplus energy [cf. Tuomi et al., 1983]). If energy allocation to present reproduction reduces future reproductive success,

then this cost of reproduction will result in the evolution of life histories that are characterized by intermediate levels of survival and reproduction (Williams, 1966).

The first explicit formulation of a present cost to future reproductive success was developed by Williams (1966). He partitioned RV into that portion available for present reproduction (i.e., present fecundity) and that attributable to future reproduction, residual reproductive value (RRV). Thus, the influence of reproductive costs on either future survival or future fecundity will strongly influence the effort an individual expends on present reproduction (Williams, 1966).

The genetic basis for reproductive costs was first explored by Medawar (1952) and Williams (1957). In discussing the evolution of senescence, they argued that selection may favour a gene having beneficial effects early in life even if the gene greatly reduces fitness later in life. Williams' (1966) later formulation of RRV extended this theory of antagonistic pleiotropy to reproductive effort. He asserted that fitness will be maximized through intermediate expenditures of effort if the beneficial effects of a gene on current reproductive success are opposed by the deleterious effects of that gene on the probability of future reproduction. There is good evidence that reproductive costs exist at the genetic level (as indicated by a negative additive genetic covariance between

present fecundity and future survival) (Rose and Charlesworth, 1981; Reznick, 1985; Bell and Koufopanou, 1986; Partridge, 1989).

Reproductive costs are difficult to quantify (Hirshfield and Tinkle, 1975; Partridge and Harvey, 1985; Reznick, 1985; Partridge and Harvey, 1988; Partridge, 1989) and attempts to do so have led to ambiguous results (Bell and Koufopanou, 1986). Some of the problems associated with measuring costs are methodological (e.g. use of inbred or clonal lines in the laboratory; field comparisons of individuals that differ phenotypically in a way that affects both their ability to survive and to reproduce). However, some of the conflicting results may be due to environmental variability in resources. Bell and Koufopanou (1986) suggested that the probability of finding negative phenotypic correlations between major components of fitness was related to the quality (in terms of food abundance) of the environment in which the organisms were studied. This is likely to be the case if the magnitude of reproductive costs is modified primarily by an extrinsic factor (e.g. density, food supply, temperature). Thus, reproductive costs need not be species-specific and may vary among populations.

The shape of the function relating reproductive effort to reproductive cost can strongly influence life history evolution (Calow, 1979; Bell and Koufopanou, 1986). This is

implicit in all theories that are based on the existence of reproductive costs (e.g. Cody, 1966; Williams, 1966; Charnov and Krebs, 1973). Different shapes of cost functions can lead to the evolution of either iteroparity or semelparity or to some combination of the two reproductive strategies (Gadgil and Bossert, 1970; Schaffer, 1974a,b; Schaffer and Rosenzweig, 1977; Bell, 1980). Although cost functions are central to life history theory, few have been empirically described. The relationship between probability of future survival and present age-specific fecundity for the rotifer Asplanchna brightwelli is negative (Snell and King, 1977) and although it is convex upward it does not depart significantly from linearity (Bell, 1980). A similarly shaped cost function exists between fraction of repeat spawners and annual production of eggs among populations of American shad, Alosa sapidissima, (Bell, 1980). Law (1979a) presented data for the annual meadow grass, Poa annua, that conformed to a negative cost function that was concave upward. Koufopanou and Bell (1984) reported a negatively linear relationship between survival and fecundity for Daphnia pulex. If the environment can influence the magnitude of reproductive costs, it may also have some effect on the shape of the cost functions.

1.2 Empirical Tests of Life History Theory

Empirical tests of life history theory have been disparate with regard to the scale at which they have been conducted. By scale, I refer to the taxonomic (e.g. species, genus, order), ecological (e.g. individuals, populations, communities) and geographical (e.g. within and between latitudes) levels of investigation. The choice of an appropriate scale is probably the single most important criterion by which life history studies are deemed to constitute valid tests of the theory.

The most common approach to testing life history theory is to compare empirical patterns of trait covariation among different species with those predicted by theory (e.g. Pianka and Parker, 1975; Stearns, 1983; Harvey and Clutton-Brock, 1985; Hutchings and Morris, 1985; Monk, 1985; Cook et al., 1989; Gittleman, 1986; Zammuto, 1986; Fleming and Gross, 1990). Charlesworth (1980) noted that multiple ecological differences in such comparisons may make it difficult to identify the factors that are truly responsible for observed life history variation. His point is an important one that can be extended to large-scale (e.g. latitudinal) comparisons of life history differences among populations of the same species (e.g. Tinkle and Ballinger, 1972; Schaffer and Elson, 1975; Leggett and Carscadden, 1978). Depending on the questions being addressed, species

and latitudinal comparisons can violate a major facet of the comparative method. That is, differences among groups are not comparable without information about differences within groups. Thus, conclusions about variation among species, or among populations at different points along a cline, are valid only when contrasted with variation within species, or among populations within a small geographical area along the cline of interest, respectively.

Small-scale population comparisons have provided some of the best empirical tests of life history theory. A good example is that on the impact of predation on life history variation in guppies, Poecilia reticulata (Reznick, 1982, 1983; Reznick and Endler, 1982; Reznick and Bryga, 1987). Guppy populations in northeastern Trinidad vary in predation intensity (from high intensity on adults, through moderate intensity on juveniles, to low intensity on both adults and juveniles) and in life history (e.g. reproductive allotment, inter-brood intervals, number and size of offspring). Many of the observed, genetically-based life history differences among guppy populations can be explained by differences in age- and size-specific mortality that are effected primarily by variation in predation intensity. Other population comparisons that quantified demographic parameters, approximated reproductive investment, and identified the environmental factor likely to be responsible for effecting the observed life history variation are those on the lizard

Sceloporus jarrovi (Ballinger, 1979), the meadow grass Poa annua (Law et al., 1977; Law, 1979 a,b), and Columbian ground squirrels Spermophilus columbianus (Dobson and Murie, 1987; Murie and Dobson, 1987).

1.3 Objectives and Overview

If life histories evolve by natural selection as a result of gene frequency changes within populations, then tests of the theory should be made by comparing the life histories of conspecific populations which are subject to different age-specific rates of survival and fecundity (Ballinger, 1979; Charlesworth, 1980; Reznick, 1985). Ideally, such tests should be conducted on a small geographical scale to minimize biogeographic variability and would compare genetically distinct populations that are members of biotically similar communities.

The brook trout, Salvelinus fontinalis, is an appropriate organism for such tests. Trout occur in a wide range of habitats within small geographical areas (Scott and Crossman, 1973), exhibit considerable and easily quantifiable life history variation (Power, 1980) and, in Newfoundland, frequently occur either alone or with the threespine stickleback, Gasterosteus aculeatus, (Scott and Crossman, 1964), a small fish (50-60 mm) which probably

neither preys on nor competes with the brook trout (seq. Scott and Crossman, 1973).

The study populations inhabit several small rivers on Cape Race, southeastern Newfoundland, and are ideal for a comparative study. The 9 km distance between the river mouths ensures minimal climatic heterogenity among systems. Brook trout are the sole salmonid in the rivers and with few exceptions they are the only fish in the rivers. Thus, the potentially confounding influences of interspecific competition and predation on life history are negligible. Population boundaries are discrete with no possibility of migration between rivers. Finally, the populations are subject to minimial exploitation and the rivers have never been stocked artificially with fish.

I combined field studies, laboratory experiments, and empirically-based model simulations to study population variation in brook trout life histories. My general objectives were (1) to describe population variation in brook trout life histories on a small geographical scale, (2) to use the comparative method in concert with laboratory manipulations to explain empirical patterns of trait covariation, (3) to identify the environmental factor(s) responsible for effecting any observed inter-population life history differences, and (4) to test empirically predictions of life history theory that address the evolution of age- and size-specific reproductive strategies and costs of

reproduction. These predictions are: (1) that costs of reproduction exist and increase with reproductive effort (Gadgil and Bossert, 1970; Bell, 1980); (2) that reproductive costs are directly related to resource abundance (Bell and Koufopanou, 1986); (3) that slow growth favours delayed maturity at a small size (Alm, 1959; Stearns and Koella, 1986); (4) that offspring size and number depends on the relationship between offspring size and survival and on the influence this relationship has on maternal fitness (Svärdson, 1949; Lack, 1954; Smith and Fretwell, 1974); (5) that egg size is inversely related to food abundance (Sibly and Calow, 1983); and (6) that selection favours the production of variable-sized offspring in unpredictable, temporally-varying environments (Kaplan and Cooper, 1984).

Chapter Two

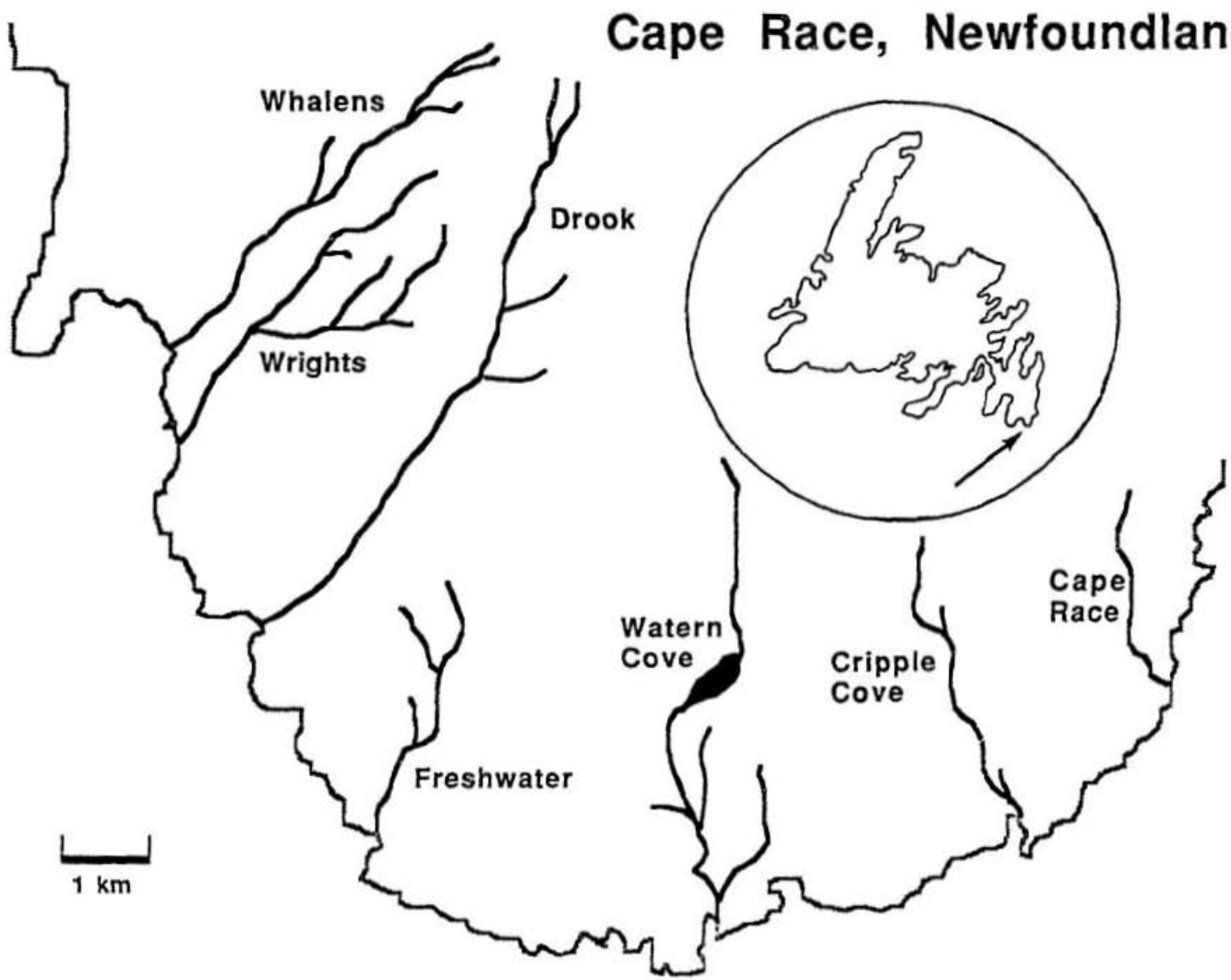
MATERIALS AND METHODS

2.1 Study Area

The study area was located on Cape Race (an area of 120 km^2; bounded by 53°16'W, 46° 45'N, 53°04'E, and 46°38'S) in south-eastern Newfoundland (Fig. 1). The cape is an almost treeless region of sub-Arctic tundra (primarily peat and blanket bog) with a vegetation dominated by ericaceous shrubs, sedges and mosses.

Seven rivers on Cape Race were included in the study. From east to west, these were Whalens River, Wrights River, Drook River, Freshwater River, Watern Cove River, Cripple Cove River, and Cape Race River. With the exception of a small (140 ha) pond on Watern Cove River, lakes and ponds were absent in these narrow (1-5 m width), short (3-6 km axial length) streams. Brook trout were the sole salmonid and, with few exceptions (a small population of threespine stickleback, Gasterosteus aculeatus, in Cripple Cove and few American eels, Anguilla rostrata, in Watern Cove and Drook), they were the only fish in these streams. There was no evidence of avian predation in any of the rivers. Because of the 12-20 metre cliffs at the river mouths that prevented

FIGURE 1. Brook trout study populations on Cape Race, southeastern Newfoundland, Canada.


Cape Race, Newfoundland
Whalens
Drook
Wrights
Watern Cove
Cripple Cove
Cape Race
Freshwater
1 km

upstream migration from the sea, all populations were nonanadromous.

All fish in this study were collected with a Smith-Root® Model 12 back-pack Electrofisher.

2.2 Population Variation in Life History

Samples of sexually mature male and female brook trout (minimum sample size of 40 for each sex) were collected from the seven rivers during the first two weeks of October in 1987 and in 1988. In 1987, sampling was conducted within 500 m length stream sections selected at random from the first 3 km of each stream (beginning at the stream mouth). This resulted in samples being taken from the first 1.5 km in five rivers (Freshwater, Drook, Cape Race, Whalens, Wrights) and from the first 2-3 km in Cripple Cove and Watern Cove rivers. Three of these populations (Freshwater, Cripple Cove, and Watern Cove) were re-sampled in 1988. These collections were made from the first 1.5 km of each stream. All individuals were frozen at -4°C shortly after capture.

Six life history traits were measured for each female and three were measured for each male. Two indices of size at maturity were measured: fork length (measured to the nearest mm) and total body weight (to the nearest 0.01 g). To determine age at maturity, scales were removed from the

left side of each fish between the base of the dorsal fin and the lateral line and mounted on acetate slides. Annuli were counted under a microfiche reader at 40X magnification. Gonads were removed from each female and weighed to the nearest 0.01 g (gonad weights from males are unreliable because male salmonids vary their sperm production throughout the spawning season [Kazakov, 1981]). Fecundity was measured as the absolute number of eggs in each female. Egg size was calculated to be the mean diameter (measured to the nearest 0.01 mm, using vernier calipers) of 10 eggs chosen at random from each female.

The selection of populations for re-sampling in 1988, and for more intensive study, was based on the criterion that they be representative of the most divergent life histories among the Cape Race populations. A disjoint cluster analysis based on Euclidean distances (FASTCLUS procedure; SAS/STAT, 1988) was used as an exploratory procedure to group all 1987 females into one of seven clusters, irrespective of their population of origin. Six variables were used in the analysis: length at maturity, total weight at maturity, gonad weight, age at maturity, egg size, and fecundity. I removed the effects of body size on each trait from the analysis by subtracting α_i x total weight (α_i is the slope of the linear regression of the ith trait on total body weight) from the ith trait on each individual. The means and variances of all variables were

standardized to 0 and 1, respectively, because the variables were not measured in the same units. A canonical discriminant analysis (CANDISC procedure; SAS/STAT, 1988) was then used to derive canonical variables for plotting the clusters in canonical space. Because there was no a priori basis for predicting that one population's life history would differ from another, population means for each trait were compared using Scheffé's method for unplanned comparisons (Sokal and Rohlf, 1981:253).

Three indices of female reproductive allotment were compared among the four populations chosen for intensive study: Freshwater, Cape Race, Cripple Cove, and Watern Cove. Analyses of covariance (GLM procedure; SAS/STAT, 1988) were used to test for differences in the slopes and the intercepts of linear regression equations that related (1) gonad weight to somatic weight, (2) fecundity to body length, and (3) egg size to body length. Comparisons of regression slopes and intercepts were planned comparisons (Sokal and Rohlf, 1981:232). That is, populations were compared singly or as groups.

2.3 Variation in Stream Habitats

For each of the streams chosen for intensive study, I quantified hydrographical differences throughout the first 1800 metres upstream of the mouth. Within 30 m long

stations, stream width was measured 0, 15 and 30 metres from the downstream end of the section. Stream depths were recorded at each width transect at intervals which corresponded to 1/4, 1/2 and 3/4 the stream width. The relative abundance of five different habitats were estimated by visual inspection within each of the 30 m long sections. Habitat types were based on differences in depth and water velocity and included: riffle (velocity (v) > 38cm s^{-1}, depth (d) < 23 cm), run (v>38 cm s^{-1}, d>23 cm), flat (v<38 cm s^{-1}, depth<46 cm), shallow pool (v<38 cm s^{-1}, d=46-68 cm), and deep pool (v<38 cm s^{-1}, d>68 cm).

A oneway ANOVA (ONEWAY procedure; MINITAB 7.2) was used to examine stream differences in depth, width, and relative abundance of habitat types. For these analyses, probability distributions of the F-statistic were constructed for each analysis by iterating the ANOVA 100 times on data that were randomized during each iteration. Stream differences were evaluated using unplanned comparisons.

2.4 Population Variation in Individual Growth

Individual growth was determined from a series of collections made from June to October, 1988, in Freshwater, Cripple Cove, Cape Race, and Watern Cove rivers. Ages were calculated such that age=0 is the time of fertilization (i.e., October) and such that ages 1 through 6 represent

individual ages at the time of reproduction. Thus, an individual spawning at the end of its second year is of age=2 (this corresponds to an age of 1+ in the fisheries literature).

Growth of fry (individuals in their first year of life) was determined from a series of four collections made in June, July, August, and October. A one-way ANOVA (planned comparisons; GLM procedure; SAS/STAT, 1988) was used to assess population differences in fry sizes (fork length) at given ages.

Population differences in individual growth throughout all age classes were assessed from June collections made at either 3 or 4 stations in each river. Length data were pooled across stations when length frequency distributions were independent of station location within each river. The G-test for goodness of fit (Sokal and Rohlf, 1981) was used to test the null hypothesis that length frequency distributions did not differ among stations within populations. Cell frequencies exceeded five in all analyses.

Population differences in individual growth rate were assessed by testing for heterogenity among the slopes of the linear regressions relating length with age in June for each of the four populations (planned comparisons). Age classes 5 and 6 were excluded from the analysis to minimize the effects that age classes having small ($n<5$) sample sizes

have on regression analyses and to ensure that growth rates were compared across the same range of ages in each population.

2.5 Population Variation in Density and Biomass

Fry inhabited relatively discrete sections of slow-moving water (0.25-2.00 m^2 in area and 15-20 cm in depth) that were usually distinct from the main body of the stream. Fry were sampled from 15 stations in Freshwater, Cripple Cove, and Watern Cove rivers on July 5, 1989. A oneway ANOVA with randomization (cf. section 2.3) was used to examine population differences in fry density.

Densities of older fish in Freshwater, Cripple Cove, Cape Race, and Watern Cove rivers were measured on three separate occasions in 1988: April 28-May 6, June 2-11, and July 16-19. The fork lengths of all fish were measured during each collection. Scales were sampled for age determination during the second period. All fish were returned to the stream sections from which they were collected. During the first two collection periods, randomly chosen sections of stream ranging from 24-57 m in length were cordoned at their upstream and downstream ends by barrier nets (7 mm square mesh). Forty to sixty percent of each section (2-4 stations in each river) was comprised of flats with the remaining habitat type being riffle.

During the third collection period, stream section length was standardized to 10 m and and three replicate pairs of contiguous riffle and flat habitat sections were chosen in each stream. Each section was completely electrofished four times from the downstream end to the upstream end. Fish density in each section was calculated to be the total number of fish collected per square metre.

Biomass (grams of fish per m^2) estimates were calculated from the lengths of older fish sampled during the third collection period. Individual weights were determined from $\log_{10}(\text{weight})$-$\log_{10}(\text{length})$ linear regressions calculated for immature males and females that were collected in October, 1987, and in October, 1988. Biomass estimates were not calculated for the other collection periods because the sampling regime during the third collection period was the most structured one and the time of the third collection period (mid-July) was nearest to the collection time of the fish for which the weight-length regressions were calculated. Differences in mean density and biomass among populations were evaluated using unplanned comparisons.

2.6 Stream Variation in Aquatic Invertebrate Biomass

Variation in secondary productivity among streams was measured by comparing the biomass of aquatic invertebrates

that colonized a series of collection bags in Freshwater, Cripple Cove, Watern Cove, and Cape Race rivers. Each bag consisted of a 45 cm length of plastic bait bag netting filled with 2.4 litres of 40 mm crushed stone. Bags were set at three randomly located stations (four replicates per station) in each river. Bags were positioned on May 19, 1989, and were retrieved on June 22-23, 1989. All invertebrates were placed in Kahle's fluid (57% distilled water, 29% ethyl alcohol, 12% formalin, and 2% glacial acetic acid) on site and were transferred to the lab where their wet weights were recorded. Comparisons of mean invertebrate biomass among populations were planned comparisons.

2.7 Population Variation in Survival

2.7.1 Age-Specific Survival

In early June, 1988, brook trout were collected from three stations in Freshwater, Cripple Cove, and Watern Cove rivers and from four stations in Cape Race River. These stations were those of the second collection period described previously in Section 2.5. The fork lengths of all fish were measured, scale samples were mounted on acetate slides for age determination, and all fish were returned to the river.

Static life tables were constructed to estimate annual survival probabilities to age x (l_x). These estimates were then used to construct semi-logarithmic plots of the survivorship schedules that would estimate the probability of survival from May through September (i.e., summer survival).

2.7.2 Overwinter Survival

Overwinter survival probabilities were estimated from a mark-recapture study conducted from October, 1988, to April, 1989, on Freshwater, Cape Race, Cripple Cove, and Watern Cove rivers. In autumn, I sampled 1 km of each river immediately upstream of the river mouths, and the following spring, I re-sampled the same stream section plus an additional 0.5 km immediately upstream of the previous section. All mature males and females collected in the autumn were measured, marked with a sex-specific fin clip (half of either the left or right pelvic fin), and returned to the stream. Fork lengths were recorded for all immature fish. All fish that were collected the following spring were measured and inspected for evidence of a fin clip. The number of marked fish collected during the spring relative to the total number marked the previous autumn provided an estimate of post-reproductive, overwinter mortality for males and females from each of the four populations. The

estimates for mature fish were determined directly from mark-recapture experiments whereas the overwinter survival probabilities for immature fish were calculated indirectly (see section 3.6.4). G-tests were used to perform planned comparisons of overwinter survival among populations.

2.7.3 The Influence of Body Size on Overwinter Survival

The influence of body size on overwinter survival was assessed for each of the four populations by comparing the length frequency distribution of mature fish collected in autumn with the length frequency distribution of recaptured, post-reproductive fish collected in spring. The independence of the frequency distributions was assessed with a G-test.

2.8 The Influence of Egg Size on Embryonic Survival and Development

Sexually mature males and females were collected from three streams in October, 1988, and were transferred to holding facilities at the Ocean Science Centre near St. John's. Eggs from 66 broods (15 from Freshwater, 27 from Cripple Cove, and 24 from Watern Cove) were fertilized (within-population crosses) in the lab. Broods were incubated separately in four vertical incubation chambers

receiving a continuous flow of water at 7.5 ± 1.0°C. Eggs were inspected daily to the developmental stage of yolk sac resorption.

A dissecting microscope fitted with an eyepiece micrometer was used to measure the egg diameters and the offspring lengths (both to the nearest 0.01 mm) of 10 randomly chosen individuals in each brood. Mean egg diameter for each brood was determined from water-hardened eggs at the time that the eggs were placed in the incubation chambers. Mean size at hatching was calculated after all eggs in a brood had hatched. Mean individual length for each brood was also measured at the time of yolk sac resorption.

Survival was measured during three stages of embryonic development: (1) fertilization to eyed stage, (2) eyed stage to hatching, and (3) hatching to resorption of yolk sac. Differences in embryonic survival and development within and among populations were evaluated with a one-way ANOVA (GLM procedure; SAS/STAT, 1988) on arc-sine transorfmed data. Pearson moment correlation coefficients were calculated between egg size and all developmental and survival characteristics.

2.9 The Influence of Egg Size and Food Abundance on Juvenile Survival

Following yolk sac resorption, 31 of the 66 broods described in section 2.8 (7 from Freshwater, 14 from Cripple Cove, and 10 from Watern Cove) were transferred to sixteen 38 litre aquaria in a temperature- (11°C) and photoperiod- (10 light:14 dark) controlled room. Twenty fish from each brood were placed in one-half of each aerated aquarium (halves were separated by gray plastic). Broods were fed twice daily under either a high (0.01 g per fish) or a low (0.005 g per fish) ration of dry pellet food (Biodiet^{R}).

Juvenile survival was monitored 20, 30, 40, and 50 days following yolk sac resorption. Survivorship was measured as the number of individuals alive in a brood at the end of a given time interval relative to the number alive at the beginning of that time interval. I analyzed for tank effects by rearing four replicates of 20 individuals from one brood (Cripple Cove population) in aquarium sections randomly located throughout the room and fed the high ration. A Model I linear regression analysis was used to relate juvenile survival to egg size. Homogeneity of slopes of the juvenile survival-egg size regression equations at each of the food levels was assessed using an analysis of covariance. The effects of aquarium origin on juvenile survival were analysed with a G-test.

Chapter Three

RESULTS

3.1 Stream Variation

3.1.1 Width and Depth

There were small differences in mean depth (range=13.56-17.07 cm) and mean width (range=3.22-4.80 m) among the four rivers selected for intensive study (Table 1). There were no significant differences in stream depth among Freshwater, Cripple Cove and Watern Cove rivers or in stream width among Freshwater, Cape Race and Watern Cove rovers. Cape Race River was significantly shallower than the other streams ($F=7.93$; $p<0.001$) while Cripple Cove was signficantly wider ($F=9.09$; $p<0.001$).

3.1.2 Habitat

The proportion of flat, riffle, and run habitat differed among streams (Table 1). The percentage of flat habitat (range=22.7-67.7%) was significantly different among the four rivers (arc-sine transformed data: $F=32.12$; $p<0.01$). Percentage of riffle habitat differed significantly among all rivers ($F=27.78$; $p<0.01$) although

Table 1. Habitat variables (means with standard deviation in parentheses) among four Cape Race rivers.

River	Depth (cm)	Width (m)	%Flat	%Riffle	%Run
Freshwater	16.82 (7.28)	3.41 (1.98)	37.0 (28.2)	51.6 (28.1)	8.1 (12.8)
Cape Race	13.56 (6.65)	3.22 (1.56)	67.7 (27.9)	26.8 (27.5)	1.1 (4.0)
Cripple Cove	17.07 (8.76)	4.80 (1.97)	55.8 (31.6)	28.7 (25.5)	5.6 (13.0)
Watern Cove	16.77 (6.45)	3.48 (1.11)	22.7 (20.1)	64.5 (26.2)	8.1 (11.5)

the percentages between Cripple Cove and Cape Race were not significant. The percentage of run habitat was significantly less in Cape Race ($F=5.42$; $p<0.01$) than it was in the other three rivers.

3.1.3 Aquatic Invertebrate Biomass

Invertebrate biomass differed significantly among streams (Table 2). There were also significant station and stream X station effects on invertebrate biomass but these accounted for less than half (28.2%) of the variation explained by stream effects (59.8%). There were no significant differences in biomass between Freshwater and Cape Race rivers (Table 3; $F=0.93$; $p=0.35$) or between Cripple Cove and Watern Cove rivers ($F=1.96$; $p=0.18$). The mean biomass of Cripple Cove and Watern Cove rivers (1.24 g m^{-2}) was three times as high as the mean biomass of Freshwater and Cape Race rivers (0.42 g m^{-2}). Mayflies (Ephemeroptera: Paraleptophebia spp.), followed by caddis flies (Trichoptera: Rhyacophila spp.), were the numerically dominant invertebrates in each stream.

3.2 Population Variation in Life History Traits

I analysed population differences in life history among fish collected in the first 1.5 km of each stream. This

Table 2. Two-way ANOVA examining the effects of stream and stream station on aquatic invertebrate biomass. (Note: stations were ordered downstream (station 1) to upstream).

Source of Variation	df	SS	MS	F
Streams	3	8.4449	2.8150	59.64
Stations	2	1.0510	0.5255	11.13
Interaction	6	2.9374	0.4896	10.37
Error	36	1.6990	0.0472	
Total	47	14.1323		

$F_{0.01[3,36]}=4.38$ $F_{0.01[2,36]}=5.25$ $F_{0.01[6,36]}=3.35$

Table 3. Stream invertebrate biomass (mean ± s.d.) in four Cape Race rivers.

River	Biomass (grams m^{-2})
Freshwater	0.39 ± 0.15
Cape Race	0.46 ± 0.20
Cripple Cove	1.10 ± 0.59
Watern Cove	1.37 ± 0.32

protocol excluded the 1987 samples from Cripple Cove and from Watern Cove. There were significant differences in life history traits between the 1987 and 1988 samples from Watern Cove and Cripple Cove but not between years for Freshwater for which both samples were made in the first 1.5 km of the river (Tables 4, 5). The 1987 and 1988 samples from Freshwater were pooled for all subsequent population analyses.

There were significant population differences in length, weight and age at maturity, egg size and fecundity among female brook trout (Table 6). The most divergent populations were Cripple Cove and Freshwater. Cripple Cove females matured at the largest size (164.1 mm; 51.61 g), had the highest number of eggs per female (153.9), and produced the second smallest eggs (4.01 mm). In contrast, Freshwater females matured at the smallest size (99.8 mm; 12.80 g), had the lowest fecundity (43.0 egg per female), but produced the largest eggs (4.43 mm). Mean age at maturity ranged from 2.62 yr for Cape Race females to 4.39 for Cripple Cove females. There were no significant differences in the mean values of the traits among Watern Cove, Wrights and Whalens populations (Table 7).

Population differences in male life histories were less than those for females (lower F values for length, weight, and age at maturity comparisons) but remained significant (Table 8). As with females, Cripple Cove males matured at

TABLE 4. Length, weight and age at maturity, egg size and fecundity of female brook trout collected in 1987 and 1988 from Freshwater, Cripple Cove, and Watern Cove rivers on Cape Race (data are means, standard deviations, and sample sizes; differences between years within populations indicated by F-statistic and associated probability, p).

	Trait				
Population	Length at maturity (cm)	Weight at maturity (g)	Age at maturity (yr)	Egg size (mm)	Number of eggs per female
Freshwater	103.6	14.31	3.45	4.47	44.5
1987	21.0	10.04	0.83	0.42	32.0
	57	57	57	56	56
Freshwater	96.8	11.32	3.10	4.40	41.8
1988	14.3	4.26	0.73	0.32	18.7
	72	58	58	58	72
F	3.70	3.29	2.87	0.65	0.03
p	0.06	0.08	0.06	0.42	0.85
Cripple Cove	136.8	30.74	3.47	3.74	74.1
1987	11.4	8.65	0.64	0.44	25.9
	40	40	40	40	40
Cripple Cove	164.1	51.61	4.39	4.01	153.9
1988	24.2	18.70	0.86	0.34	71.2
	66	49	49	48	65
F	44.55	42.36	30.93	10.55	46.30
p	<0.01	<0.01	<0.01	<0.01	<0.01
Watern Cove	115.6	18.43	2.51	4.01	47.6
1987	10.6	4.66	0.58	0.43	14.0
	69	69	68	68	68
Watern Cove	126.9	25.22	3.15	4.16	65.1
1988	14.8	9.72	1.02	0.34	29.9
	77	52	52	52	77
F	27.53	25.78	18.75	4.49	19.34
p	<0.01	<0.01	<0.01	0.04	<0.01

TABLE 5. Length, weight and age at maturity of male brook trout collected in 1987 and 1988 from Freshwater, Cripple Cove, and Watern Cove rivers on Cape Race (data are means, standard deviations, and sample sizes; differences between years within populations indicated by F-statistic and associated probability, p).

	Trait		
Population	Length at maturity (cm)	Weight at maturity (g)	Age at maturity (yr)
Freshwater 1987	96.4 15.7 47	11.68 5.96 47	3.25 0.82 47
Freshwater 1988	90.4 17.5 86	10.26 6.64 86	2.94 0.94 86
F(p)	3.35(0.09)	2.95(0.11)	2.75(0.08)
Cripple Cove 1987	123.4 15.9 58	23.61 8.94 58	2.79 0.77 58
Cripple Cove 1988	161.9 25.9 51	51.26 21.81 46	3.00 1.20 51
F(p)	89.65(<0.001)	40.08(<0.001)	77.06(<0.001)
Watern Cove 1987	120.6 15.6 51	20.22 11.45 51	2.65 0.76 51
Watern Cove 1988	127.1 21.3 45	28.38 14.76 45	3.09 1.06 45
F(p)	18.78(<0.001)	20.04(<0.001)	17.88(<0.001)

Table 6. Length, weight, and age at maturity, egg size, and fecundity for female brook trout from seven populations on Cape Race, Newfoundland (data are means, standard deviations, and sample sizes).

	Trait				
Population	Length at maturity (cm)	Weight at maturity (g)	Age at maturity (yr)	Egg size (mm)	Number of eggs per female
Freshwater	99.8	12.80	3.28	4.43	43.0
	17.8	7.80	0.81	0.37	25.3
	129	115	115	114	128
Drook	134.2	31.23	3.43	4.04	99.2
	17.7	12.62	0.66	0.50	40.8
	53	53	53	52	51
Cripple Cove	164.1	51.61	4.39	4.01	153.9
	24.2	18.70	0.86	0.34	71.2
	66	49	49	48	65
Cape Race	115.3	18.88	2.62	4.22	53.8
	9.8	4.58	0.64	0.44	25.9
	40	40	40	40	40
Watern Cove	126.9	25.22	3.15	4.16	65.1
	14.8	9.72	1.02	0.34	29.9
	77	52	52	52	77
Whalens	118.6	19.83	3.10	3.93	53.0
	10.5	4.71	0.54	0.35	14.7
	50	50	50	50	50
Wrights	118.6	20.47	3.10	4.02	54.1
	9.5	4.55	0.49	0.40	14.9
	52	52	52	52	52
F-statistic	131.91	108.63	27.79	15.56	92.98
p-value	0.0001	0.0001	0.0001	0.0001	0.0001

Table 7. Rank orders of populations based on mean values of four female life history traits (rank=1 for highest values; vertical lines include populations for which there are no significant differences among means).

Rank	Length at maturity	Weight at maturity	Age at maturity
1	Cripple Cove	Cripple Cove	Cripple Cove
2	Drook	Drook	Drook
3	Watern Cove	Watern Cove	Freshwater
4	Wrights	Wrights	Watern Cove
5	Whalens	Whalens	Wrights
6	Cape Race	Cape Race	Whalens
7	Freshwater	Freshwater	Cape Race

Rank	Egg size	Number of eggs per female
1	Freshwater	Cripple Cove
2	Cape Race	Drook
3	Watern Cove	Watern Cove
4	Drook	Wrights
5	Wrights	Cape Race
6	Cripple Cove	Whalens
7	Whalens	Freshwater

the largest size (157.1 mm; 51.26 g) while Freshwater males matured at the smallest size (92.5 mm; 10.76 g). Mean age at maturity ranged from 3.00 for Cape Race males to 4.10 for Whalens males. With the exception of males from Freshwater and Cripple Cove, there were few significant differences in life history traits among males from the other populations (Table 9).

The cluster analysis revealed a divergence of females into three groups having similar life histories (Table 10). The majority of females from each population were grouped into either one or two clusters. Ninety percent of the females in Freshwater were grouped into cluster 4. Cluster 2 included the majority of females from Cape Race (70%), Watern Cove (93%), Whalens (86%), and Wrights (65%) rivers. The third group consisted of clusters 5 and 7 which included 77% and 95% of Drook and Cripple Cove females, respectively. Thus, the populations chosen for further study - Freshwater, Cape Race, Cripple Cove, Watern Cove - were representative of each of the three life history groups.

3.3 Population Variation in Fish Density and Biomass

Fry density in fry habitat ranged from 0.15-0.31 individuals per m^2 in Freshwater, Cripple Cove, and Watern Cove rivers (Table 11). Density was significantly higher in Freshwater ($F=11.17$; $p<0.01$) than it was in the other two

Table 8. Length, weight, and age at maturity for male brook trout from seven populations on Cape Race (data are means, standard deviations and sample sizes).

	Trait		
Population	Length at maturity (cm)	Weight at maturity (g)	Age at maturity (yr)
Freshwater	92.5	10.76	3.05
	16.2	2.05	0.87
	132	132	132
Drook	136.6	35.61	3.56
	23.8	19.24	0.90
	69	69	69
Cripple Cove	157.1	51.26	3.76
	22.5	21.81	0.99
	46	46	46
Cape Race	128.6	27.25	3.00
	21.4	14.65	0.81
	56	56	56
Watern Cove	127.1	28.38	3.09
	21.3	14.76	1.06
	45	45	45
Whalens	139.4	33.28	4.10
	17.4	12.06	0.81
	40	40	40
Wrights	130.9	28.78	3.63
	13.1	8.78	0.69
	51	51	51
F	91.73	60.39	12.81
p	0.0001	0.0001	0.0001

Table 9. Rank orders of populations based on mean values of three male life history traits (rank=1 for highest values; vertical lines include populations for which there are no significant differences among means).

Rank	Length at maturity	Weight at maturity	Age at maturity
1	Cripple Cove	Cripple Cove	Whalens
2	Whalens	Drook	Cripple Cove
3	Drook	Whalens	Wrights
4	Wrights	Wrights	Drook
5	Cape Race	Watern Cove	Watern Cove
6	Watern Cove	Cape Race	Freshwater
7	Freshwater	Freshwater	Cape Race

TABLE 10. Classification of female brook trout from seven Cape Race populations in seven life history clusters.

	Population						
Cluster	Fresh-water	Drook	Cripple Cove	Cape Race	Watern Cove	Whalens	Wrights
1	0	3	1	0	0	0	0
2	0	0	0	35	64	43	34
3	5	4	1	0	0	0	1
4	51	1	0	0	0	0	3
5	0	26	9	11	3	5	10
6	1	4	0	4	2	2	2
7	0	15	29	0	0	0	0

Table 11. Density (fish m^{-2}) and length (mm) of brook trout fry in three Cape Race rivers (ranges in parentheses).

River	Number of Stations	Density (mean ± s.d.)	Length (mean ± s.d.)
Freshwater	15	0.31 0.14 (0.13-0.40)	38.1 3.6 (29-48)
Cripple Cove	15	0.15 0.04 (0.08-0.20)	37.5 4.4 (27-45)
Watern Cove	15	0.18 0.08 (0.05-0.30)	34.6 5.5 (24-48)

rivers. Fry in Watern Cove were significantly smaller ($F=8.71$; $p<0.01$) than those in Cripple Cove and Freshwater rivers.

Within rivers, population density of older fish (older than 1 year) did not differ between riffle and pool habitats (Freshwater: $F=0.60$, $p=0.48$; Cape Race: $F=0.99$, $p=0.39$; Cripple Cove: $F=1.58$, $p=0.30$; Watern Cove: $F=4.23$, $p=0.20$) (Table 12). Density data for the two habitats were pooled for population comparisons. There were no monthly differences in the density of older fish (Freshwater: $F=1.55$, $p=0.25$; Cripple Cove: $F=2.85$, $p=0.13$; Watern Cove: $F=2.12$, $p=0.18$) (Tables 12,13). Population density was significantly lower in Cape Race relative to the other rivers (mean $\pm$ s.d.$=0.25 \pm 0.08$ fish m^{-2}; $F=12.35$; $p<0.01$). There were no significant differences in density among Freshwater (0.76 ± 0.27), Cripple Cove (0.81 ± 0.28), and Watern Cove (0.93 ± 0.43) rivers ($F=0.73$; $p=0.50$).

Within rivers, biomass of older fish did not differ between riffle and pool habitats (Freshwater: $F=0.58$, $p=0.50$; Cape Race: $F=0.96$, $p=0.40$; Cripple Cove: $F=0.53$, $p=0.57$; Watern Cove: $F=3.53$, $p=0.13$). Population differences in biomass (grams m^{-2}) exceeded differences in density ($F=13.98$; $p<0.01$) (Table 14). Biomass was highest in Watern Cove (14.94 ± 4.30) and lowest in Cape Race (2.84 ± 1.25). Biomass differed significantly among Watern Cove, Freshwater and Cripple Cove ($F=5.79$; $p<0.01$) but not

Table 12. Density of brook trout (older than age 1) in flat and riffle habitats in four Cape Race rivers in July.

Population	Habitat	n	Station Area (m^2)	Density (numbers m^{-2})
Freshwater	Flat	34	25.2	1.35
		30	33.6	0.89
		29	28.7	0.87
	Riffle	13	15.4	0.84
		13	26.8	0.48
		18	27.3	0.66
Cape Race	Flat	16	43.1	0.37
		5	35.0	0.14
		7	45.6	0.15
	Riffle	8	28.7	0.28
		6	36.6	0.16
		6	34.1	0.23
Cripple Cove	Flat	25	39.8	0.63
		36	31.3	1.25
		28	56.4	0.62
	Riffle	19	32.9	0.94
		27	27.7	1.12
		26	29.2	1.06
Watern Cove	Flat	77	74.2	1.01
		37	26.3	1.41
		68	40.9	1.66
	Riffle	26	38.6	0.67
		18	17.8	1.07
		23	31.3	0.73

Table 13. Density of brook trout (older than age 1) in combined flat and riffle habitats in spring in four Cape Race rivers.

Population	Month	n	Station Area (m^2)	Density (numbers m^{-2})
Freshwater	April	36	79.3	0.45
		72	119.1	0.60
	June	108	110.5	0.98
		69	150.0	0.46
		125	163.5	0.76
Cape Race	May	63	196.3	0.32
		23	91.2	0.25
	June	43	187.8	0.23
		53	139.7	0.38
		60	215.3	0.28
		54	210.5	0.26
Cripple Cove	April	100	146.7	0.68
		85	117.0	0.73
	May	37	93.6	0.39
	June	99	147.0	0.63
		83	72.8	1.14
		90	164.4	0.55
Watern Cove	May	45	100.0	0.45
		45	109.0	0.41
	June	111	231.4	0.48
		291	334.4	0.84
		105	72.0	1.46

Table 14. Biomass (grams m^{-2}) of brook trout (older than age 1) in four Cape Race populations in July.

Population	Habitat	
	Flat	Riffle
Freshwater	10.64	10.05
	5.89	3.29
	8.13	5.71
Cape Race	5.11	3.06
	2.73	1.38
	2.21	2.56
Cripple Cove	10.01	7.75
	6.14	13.88
	17.78	14.02
Watern Cove	17.07	11.81
	19.98	19.11
	27.87	9.87

between the latter two populations ($F=4.09$; $p=0.07$).

3.4 Growth

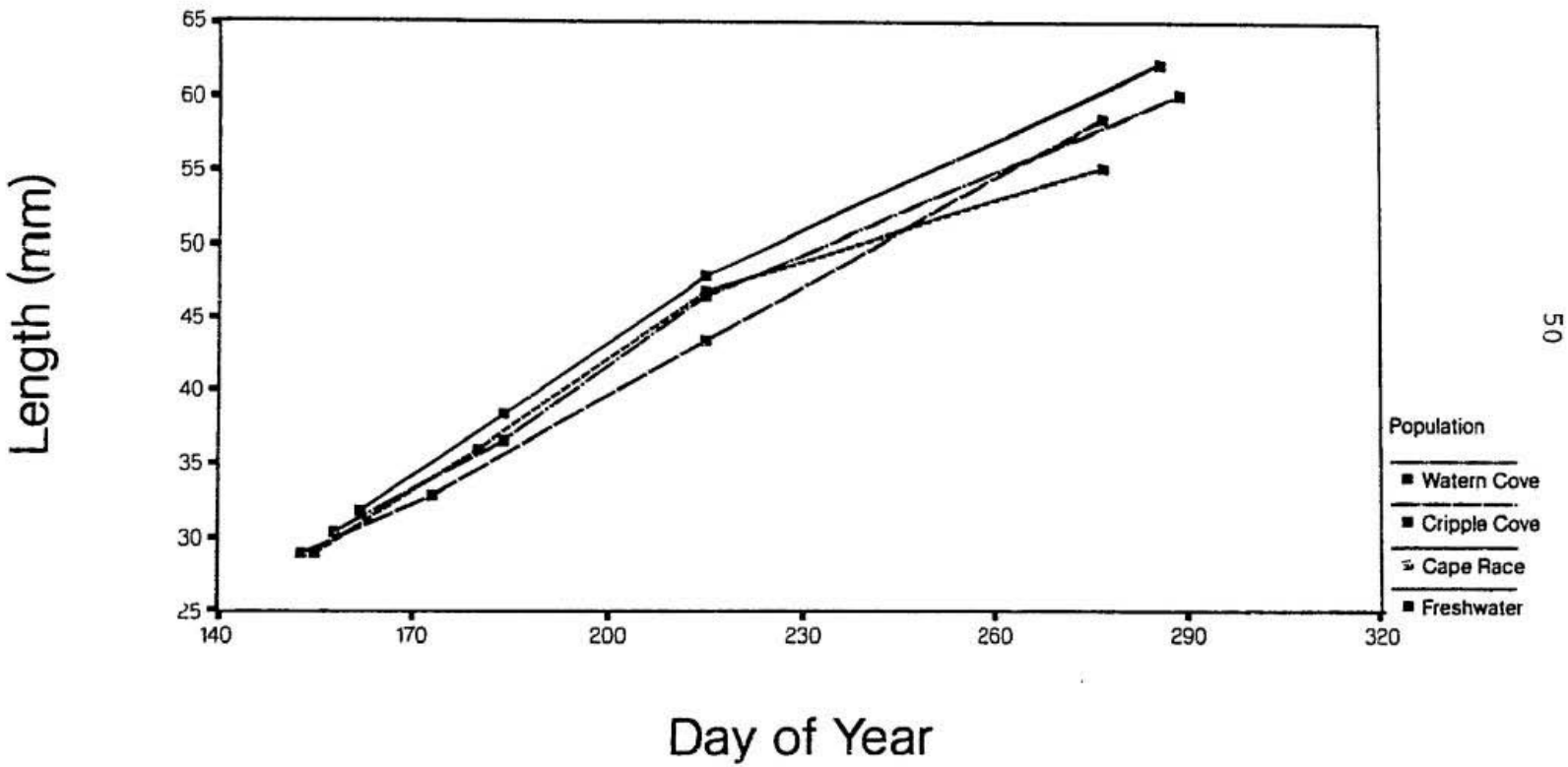
3.4.1 Growth of Fry

Population mean lengths of fry increased from 29.0-31.8 mm in early June to 43.4-47.9 mm in early August and to 55.2-62.2 mm in early to mid-October (Table 15). Growth from early June to early August generally exceeded growth from early August to mid-October (Fig. 2). Differences in growth rate were assessed by comparing mean individual lengths of fish collected on the same day. In early August, the mean length of Cripple Cove individuals was significantly less than the mean lengths of trout from Watern Cove, Freshwater, and Cape Race populations ($F=16.6$; $p<0.01$). However, trout from Freshwater had a significantly lower mean length in mid-October than trout from Cripple Cove ($F=32.62$; $p<0.01$). Thus, growth to early August was slowest in Cripple Cove and equal among the other three populations whereas growth from early August to mid-October was slowest in Freshwater (Fig. 2). With one exception, there were no significant differences ($p>0.05$) in the length frequency distributions between consecutive collection periods within rivers. The October length frequency distribution in Watern Cove was significantly different from

Table 15. Length during the first year of life of brook trout from four populations on Cape Race.

Population	Date	Day of Year	Mean Length (mm)	s.d.	n
Freshwater	Jun 4	155	29.0	3.1	78
	Jun 29	180	35.9	3.9	94
	Aug 3	215	46.8	3.5	105
	Oct 4	277	55.2	4.3	217
Cape Race	Jun 11	162	31.8	2.0	33
	Jul 3	184	38.3	3.7	100
	Aug 3	215	47.9	5.7	80
	Oct 13	286	62.2	6.7	81
Cripple Cove	Jun 2	153	29.0	3.6	133
	Jun 22	173	32.8	3.9	98
	Aug 3	215	43.4	5.0	111
	Oct 4	277	58.6	7.3	186
Watern Cove	Jun 7	158	30.4	3.2	133
	Jul 3	184	36.5	4.1	102
	Aug 3	215	46.5	4.6	100
	Oct 16	289	60.2	5.5	333

FIGURE 2. Growth during the first year of life for brook trout in four Cape Race populations.


Length (mm)
65
60
55
50
45
40
35
30
25
140
170
200
230
260
290
320
Day of Year
Population
Watern Cove
Cripple Cove
Cape Race
Freshwater

the August distribution ($G=16.54$; $X^2_{0.05[4]}=9.49$) and was skewed to the left.

3.4.2 Growth of Older Fish

There were no significant differences in length frequency distributions among stations in Freshwater ($G_{[4]}=7.96$; $p>0.05$), Cripple Cove ($G_{[6]}=10.48$; $p>0.05$), and Cape Race ($G_{[6]}=5.03$; $p>0.05$) populations. Consequently, length data were pooled across all stations in each of these populations. The significantly different length distributions from the three Watern Cove stations ($G_{[4]}=20.97$;$p<0.01$) permitted the pooling of data from stations 1 and 2 only ($G_{[2]}=3.35$;$p>0.05$).

Individuals from Freshwater, Cripple Cove and Watern Cove were represented by age classes 1-5 whereas age=5 individuals were absent from Cape Race River (Table 16). Differences in growth during the first year of life were evaluated by using a one-way ANOVA to test the null hypothesis that length at age=1 did not differ among populations. Trout in Freshwater were significantly smaller than trout in the other populations at age=1 ($F=273.48$; $p<0.0001$).

Length was positively correlated with age within each of the four populations (Table 17). The regression slope of the population having the highest individual growth rate,

TABLE 16. Lengths (mm) of brook trout in five age classes from four Cape Race populations in June.

	Age Class				
Population	1-2	2-3	3-4	4-5	5-6
Freshwater					
mean	62.6	83.4	96.2	110.7	145.5
s.d.	6.3	4.3	5.4	8.2	7.8
n	157	74	57	9	2
Cripple Cove					
mean	74.3	112.4	139.2	165.5	183.0
s.d.	8.3	11.2	7.6	6.3	0
n	155	76	28	10	2
Cape Race					
mean	84.5	116.3	133.6	160.0	
s.d.	6.9	6.9	3.1	-	
n	127	71	11	1	
Watern Cove					
mean	74.8	107.2	129.8	149.1	179.3
s.d.	7.6	8.4	7.1	5.7	10.7
n	179	117	78	17	3

TABLE 17. Parameter estimates (slope and intercept), R^2, and sample size (n) for linear regression equations relating length to age during the first three years of life in four Cape Race brook trout populations (all regressions are significant: $p<0.0001$).

Population	Slope	Intercept	R^2	n
Freshwater	17.41	45.82	0.84	288
Cripple Cove	34.16	40.95	0.86	259
Cape Race	27.93	57.56	0.84	209
Watern Cove	28.00	48.72	0.85	374

Cripple Cove, was almost twice (196%) that of the population having the slowest growing individuals, Freshwater. There was significant slope heterogeneity when all four populations were included in the analysis ($F=47.44$; $p=0.0001$). Although the regression slopes for Cape Race and Watern Cove populations were homogeneous ($F<0.01$; $p=0.96$), the intercept for the Cape Race regression equation was significantly greater than that for Watern Cove ($F=30.33$; $p=0.0001$), i.e., Cape Race fish were longer at age=1 than those in Watern Cove.

3.5 Population Variation in Reproductive Effort

3.5.1 Reproductive Allocation

There were significant population differences among the slopes of the regressions relating gonad weight to somatic weight ($F=5.25$; $p=0.002$; Figs. 3,4,5). Slopes were similar between Freshwater and Watern Cove populations ($F=1.07$; $p=0.30$) and among Cape Race, Watern Cove, and Cripple Cove populations ($F=2.20$; $p=0.11$) although there were significant differences in intercepts for both comparisons ($F=124.78$; $p=0.0001$ and $F=182.43$; $p<0.0001$, respectively) (Table 18). Females from Freshwater allocated proportionately the most body tissue to gonads. For example, for 20 g of somatic weight, Freshwater females allocated an average 45 to 135%

FIGURE 3. Linear regressions relating gonad weight to somatic weight in four brook trout populations on Cape Race.

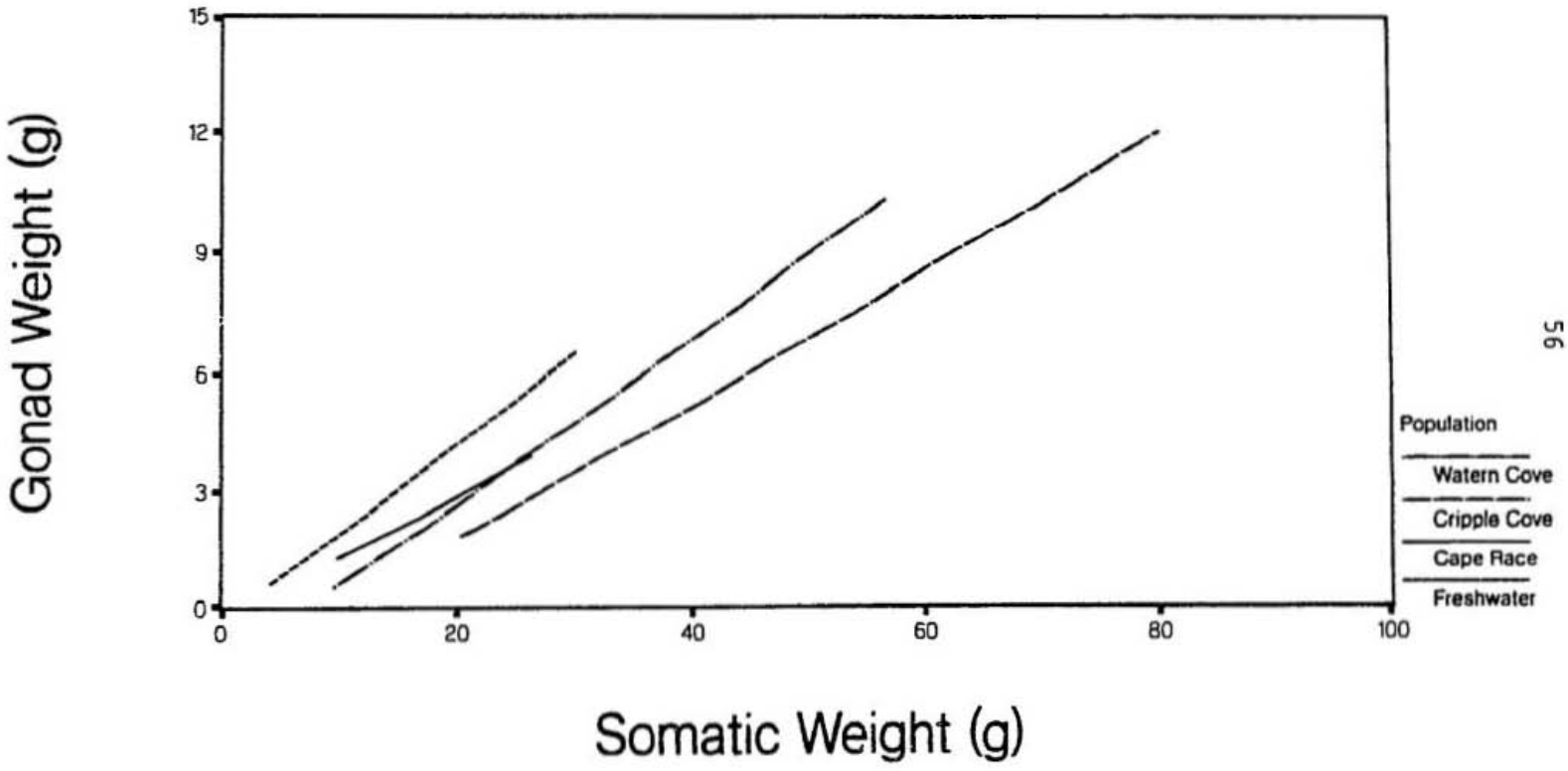
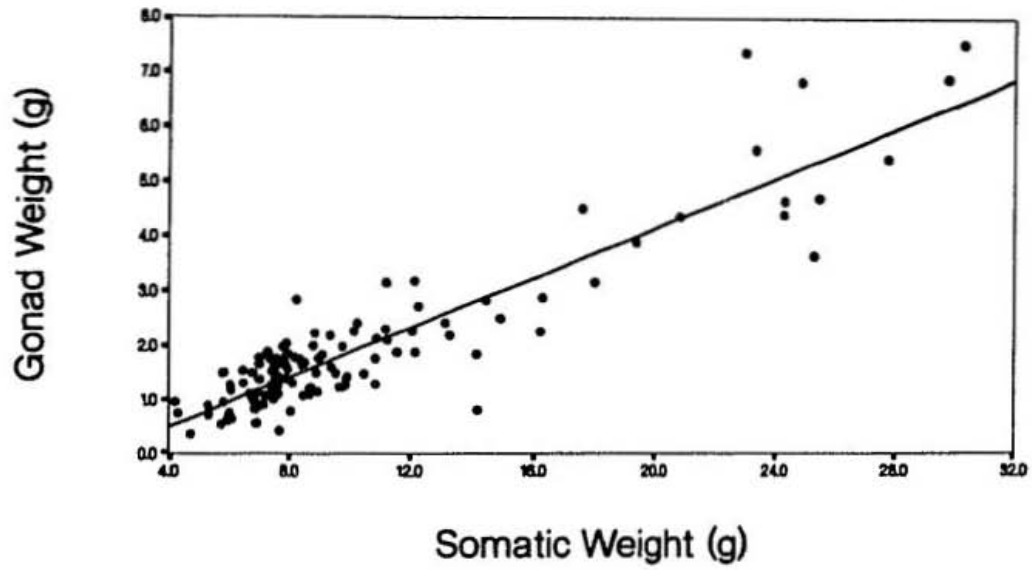

Gonad Weight (g)
15
12
9
6
3
0
0
20
40
60
80
100
Somatic Weight (g)
Population
Watern Cove
Cripple Cove
Cape Race
Freshwater

FIGURE 4. Relationship between gonad weight and somatic weight in Freshwater and Cape Race populations. (Note: axes at different scales.)

Freshwater



Cape Race

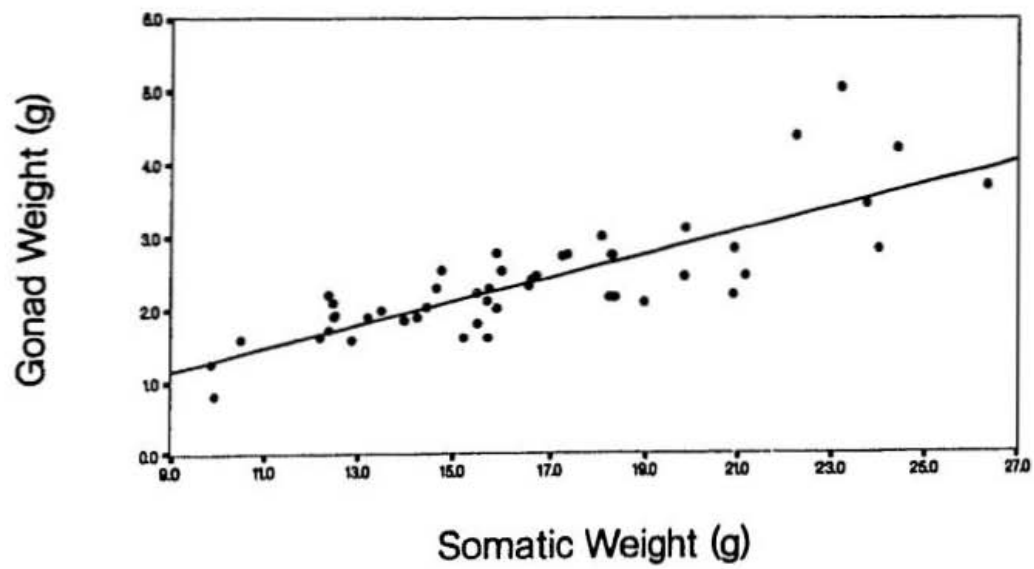
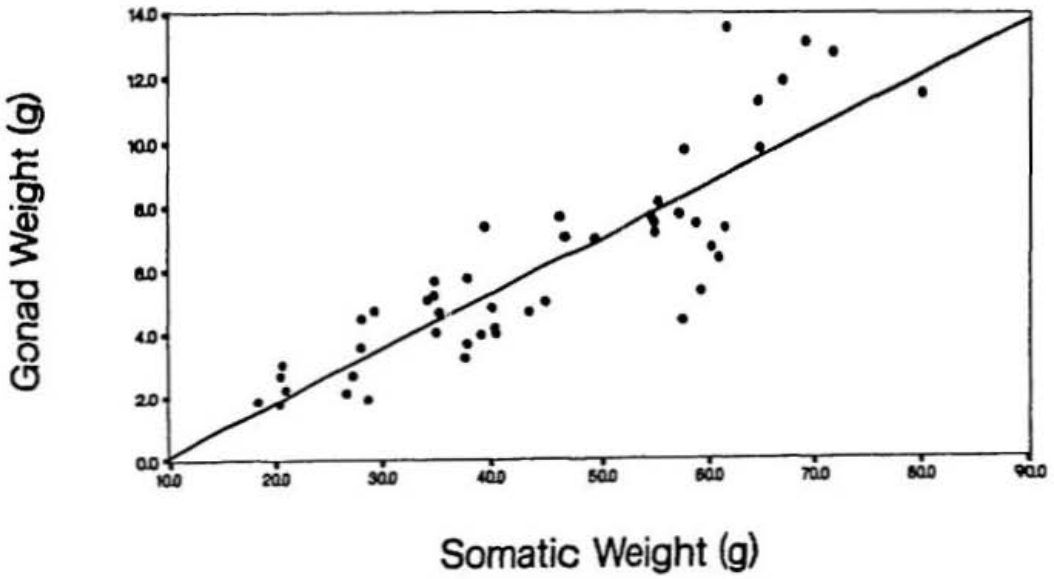


FIGURE 5. Relationship between gonad weight and somatic weight in Cripple Cove and Watern Cove populations. (Note: ordinates at different scales.)

Cripple Cove



Watern Cove

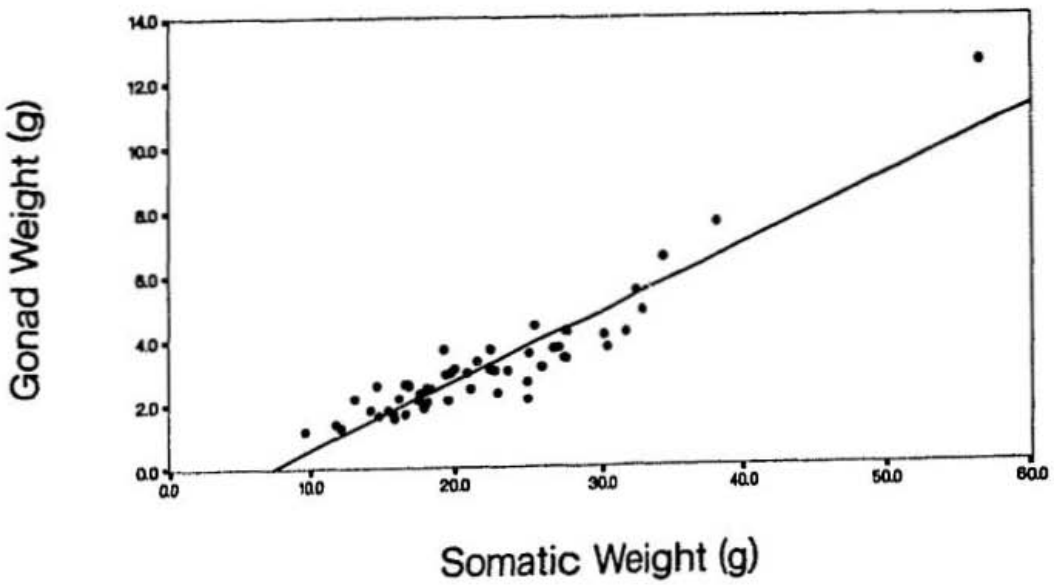


Table 18. Parameter estimates for linear regression equations relating somatic weight to gonad weight and maternal length to egg size and fecundity in four brook trout populations on Cape Race (values are slopes above intercepts; r in parentheses).

Population	Gonad weight (g)	Egg size (mm)	Number of eggs per female
Freshwater	0.23	0.012	1.11
	-0.40	3.203	-68.25
	(0.93)	(0.57)	(0.80)
Cape Race	0.16	0.021	0.63
	-0.31	1.830	-18.57
	(0.82)	(0.60)	(0.48)
Cripple Cove	0.17	0.006	2.66
	-1.61	2.962	-280.66
	(0.87)	(0.39)	(0.80)
Watern Cove	0.21	0.018	1.30
	-1.53	1.880	-100.14
	(0.93)	(0.77)	(0.64)

more tissue to gonads than females from the other three populations (Table 19).

One approximation of reproductive effort is the proportion of total body weight allocated to gonads (this proportion is termed the gonado-somatic index or GSI in the fisheries literature). Mean GSI varied by 60% among populations and ranged from 0.10 (Cripple Cove) to 0.16 (Freshwater) (Table 20). The GSI for Freshwater females was significantly greater than those of the other three populations ($F=44.91$; $p<0.001$). GSI was weakly, but significantly, correlated with body size in all populations save that from Cape Race (Table 20; Figs. 6,7,8).

3.5.2 The Effect of Maternal Size on Fecundity and Egg Size

Fecundity was positively correlated with maternal length within populations (Table 18; Figs. 9,10,11). Significant slope heterogeneity existed among the population regressions relating fecundity to body length ($F=25.53$; $p=0.0001$). When the population having the highest slope and greatest length range (Cripple Cove) was excluded from the analysis of covariance (Table 18), there were no significant differences among the slopes of Freshwater, Cape Race, and Watern Cove regressions ($F=2.92$; $p=0.06$), although significant differences did exist among their intercepts ($F=43.64$; $p=0.0001$). A 122 mm long female from Freshwater

Table 19. Standardized measures of gonad weight, egg size, and fecundity among four Cape Race brook trout populations (gonad weight is standardized to a somatic weight of 20 g; egg size and fecundity are standardized to a body length of 122 mm).

Population	Gonad Weight (g)	Egg Diameter (mm)	Egg Volume (mm^3)	Fecundity (Number of eggs per female)
Freshwater	4.20	4.67	53.3	67.2
Cape Race	2.89	4.39	44.3	58.3
Cripple Cove	1.79	3.69	26.3	43.9
Watern Cove	2.67	4.08	35.6	58.5

Table 20. Mean gonado-somatic index (GSI) and regression parameters relating GSI to body length for females in four Cape Race brook trout populations (standard deviation in parentheses).

Population	GSI	Slope	Intercept	R^2	p
Freshwater	0.16 (0.04)	0.0005	0.1124	0.05	0.01
Cape Race	0.12 (0.02)	0.0003	0.0937	0.00	0.35
Cripple Cove	0.10 (0.02)	0.0006	0.0248	0.17	0.002
Watern Cove	0.12 (0.02)	0.0006	0.0467	0.15	0.003

FIGURE 6. Linear regressions relating gonado-somatic index (GSI) to maternal length in four brook trout populations on Cape Race.

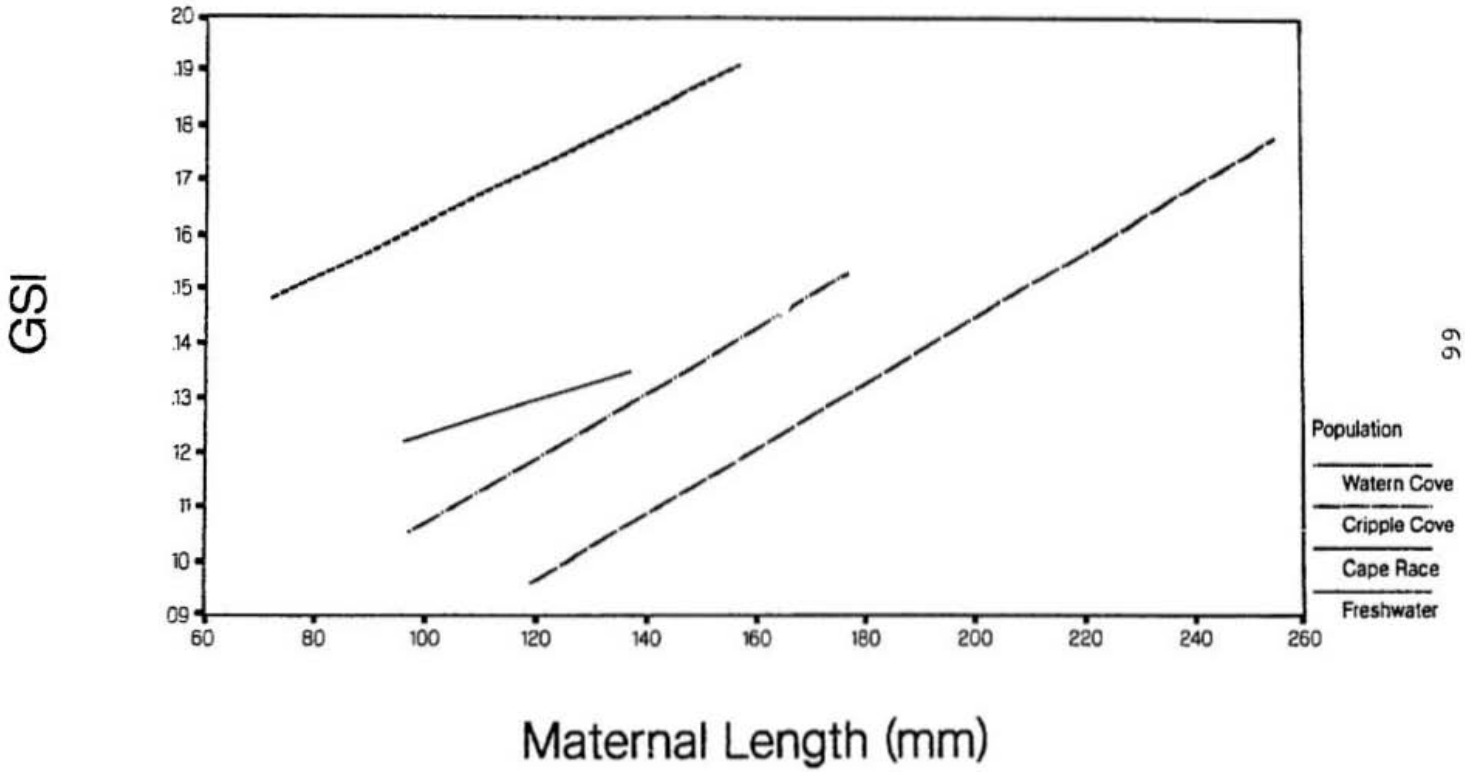
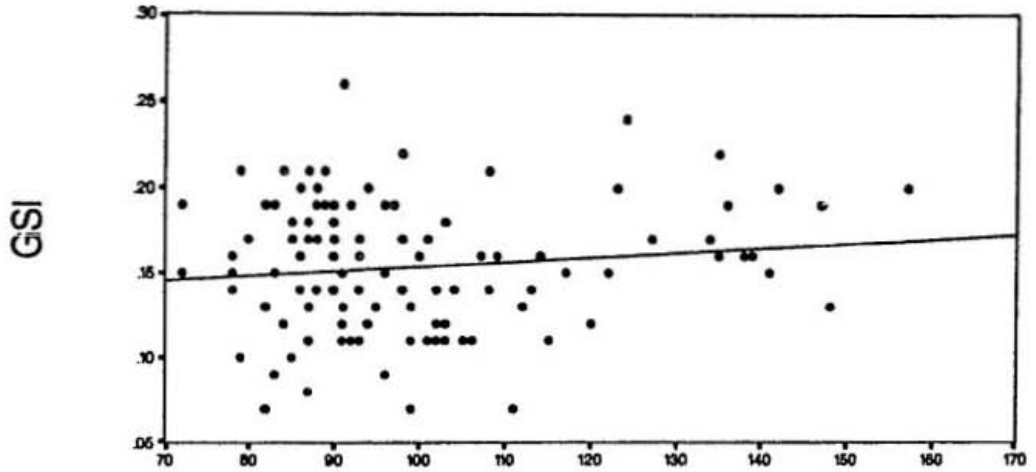

GSI
20
19
18
17
16
15
14
13
12
11
10
09
60
80
100
120
140
160
180
200
220
240
260
Maternal Length (mm)
Population
Watern Cove
Cripple Cove
Cape Race
Freshwater

FIGURE 7. Relationship between GSI and maternal length in Freshwater and Cape Race populations. (Note: axes at different scales.)

Freshwater



Cape Race

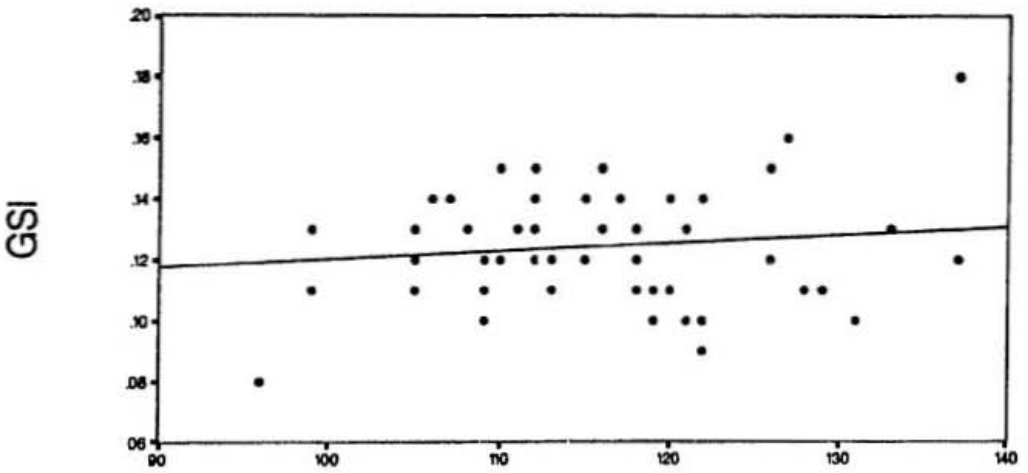
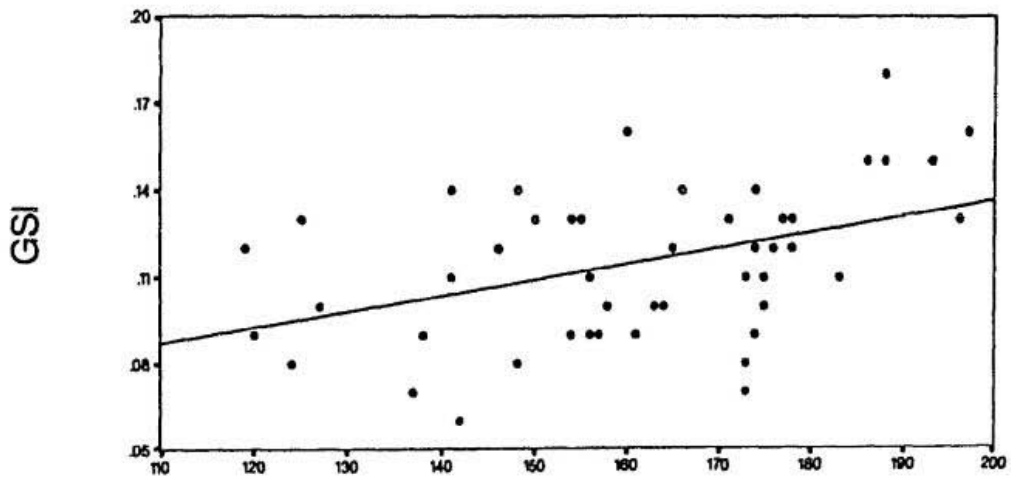


FIGURE 8. Relationship between GSI and maternal length in Cripple Cove and Watern Cove populations. (Note: axes at different scales.)

Cripple Cove



Watern Cove

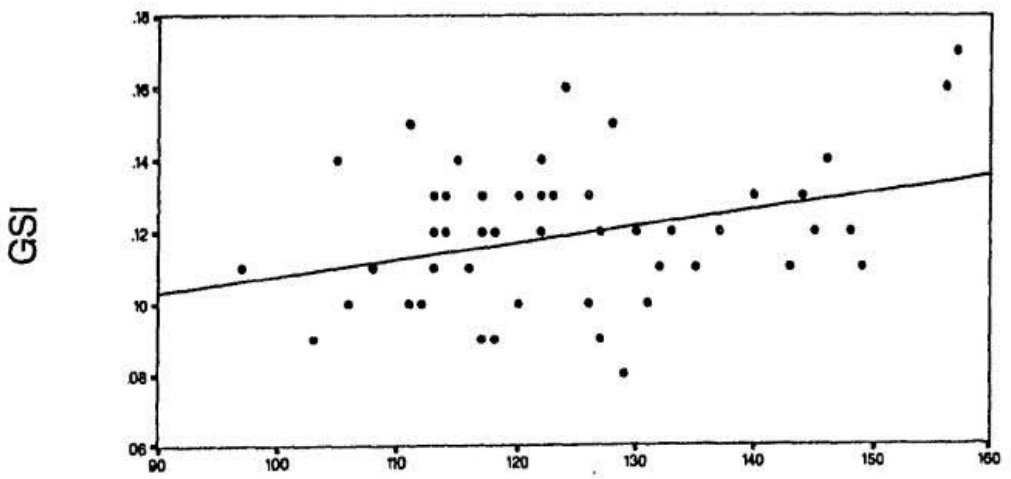


FIGURE 9. Linear regressions relating fecundity to maternal length in four brook trout populations on Cape Race.

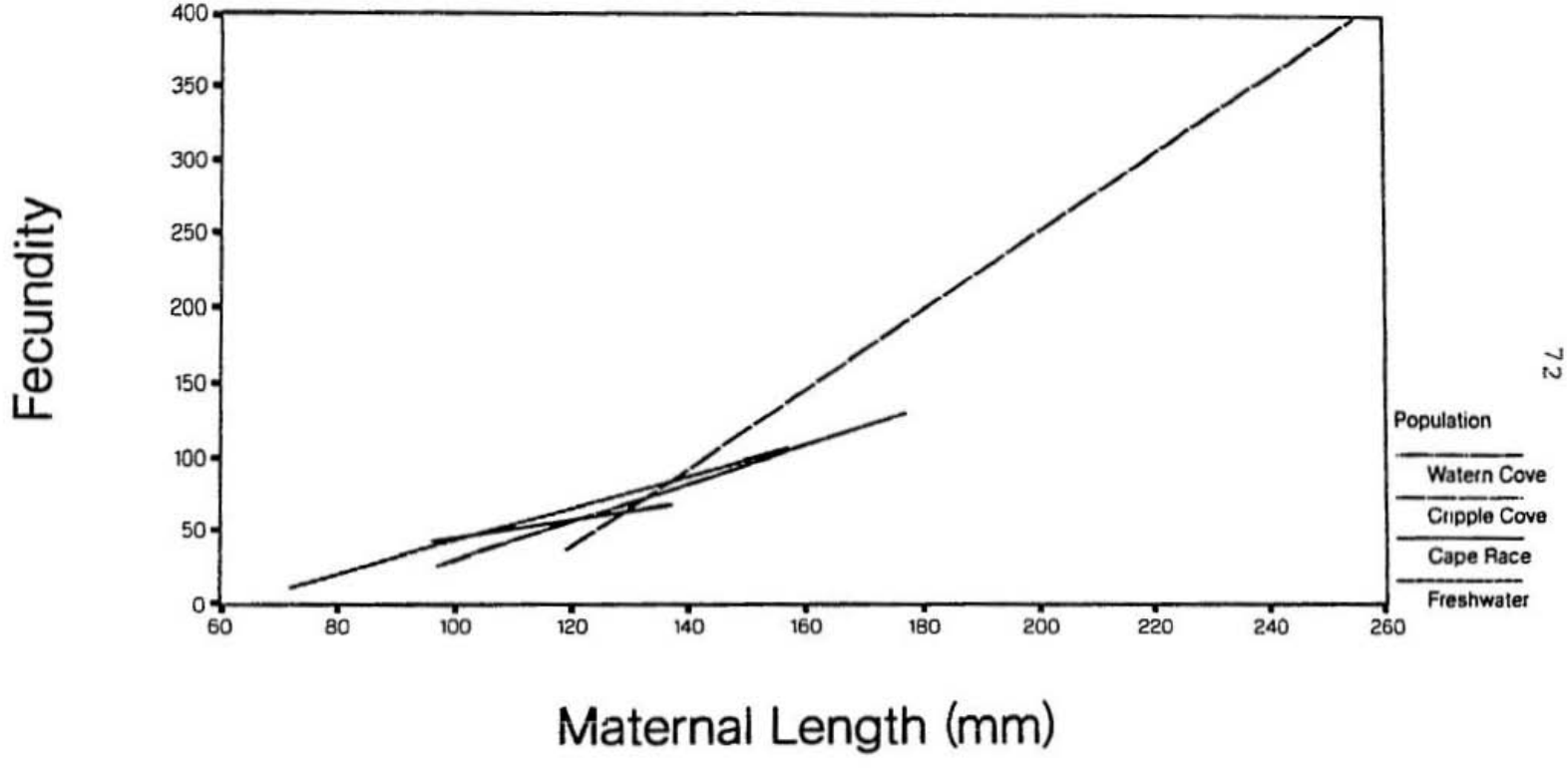
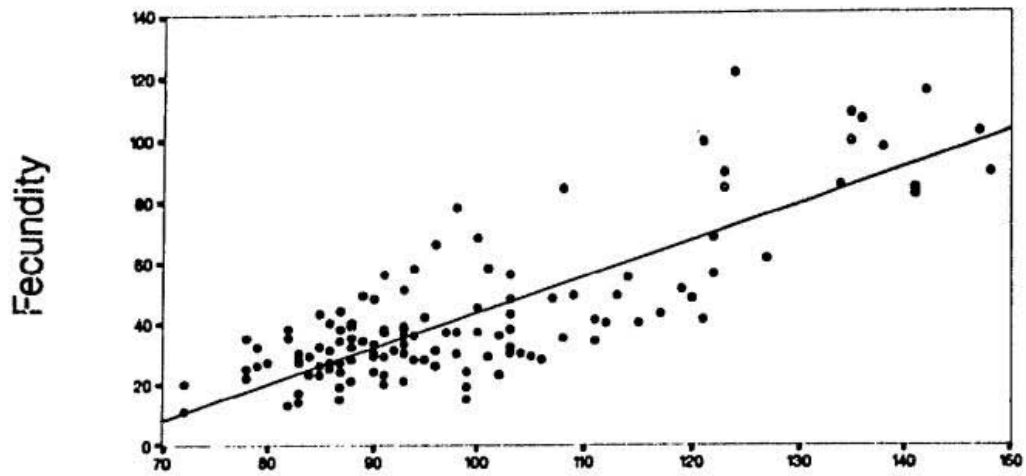

Fecundity
400
350
300
250
200
150
100
50
0
60
80
100
120
140
160
180
200
220
240
260
Maternal Length (mm)
Population
Watern Cove
Cripple Cove
Cape Race
Freshwater

FIGURE 10. Relationship between fecundity and maternal length in Freshwater and Cape Race populations. (Note: axes at different scales.)

Freshwater



Cape Race

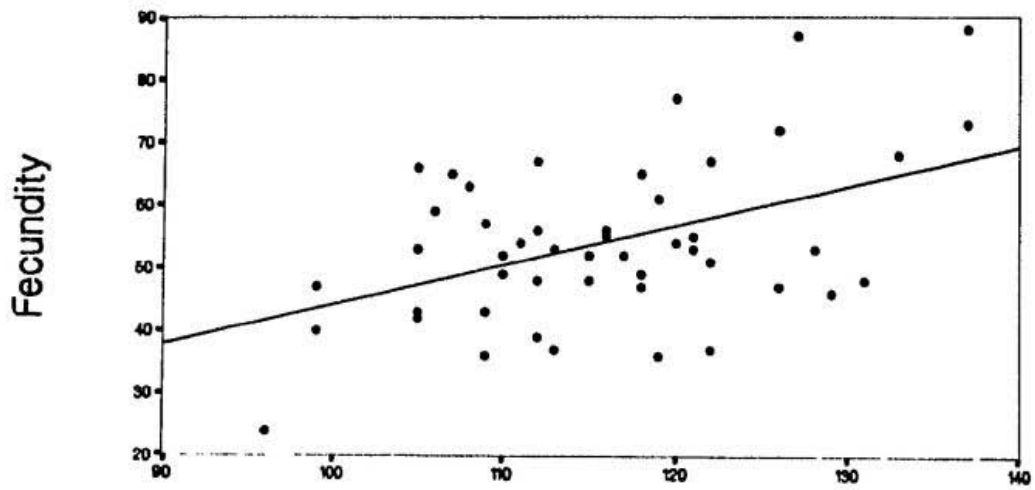
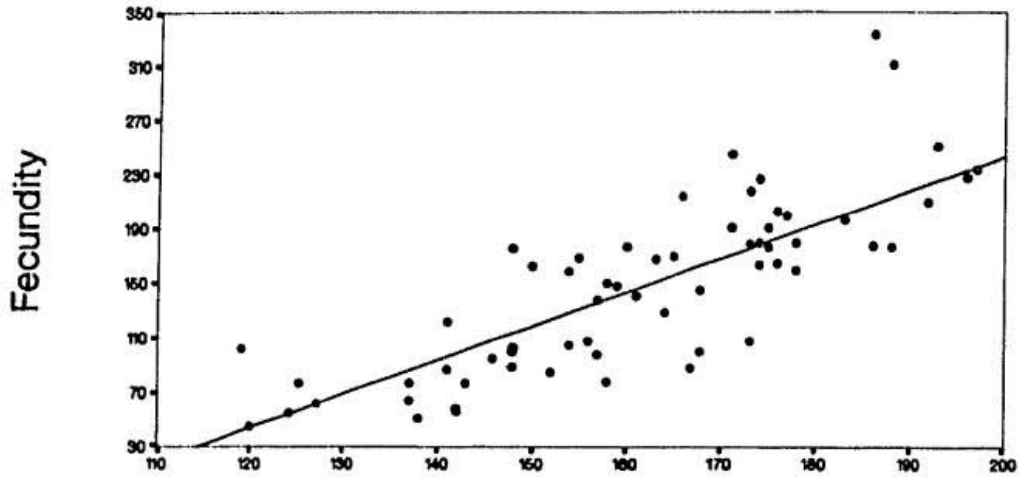
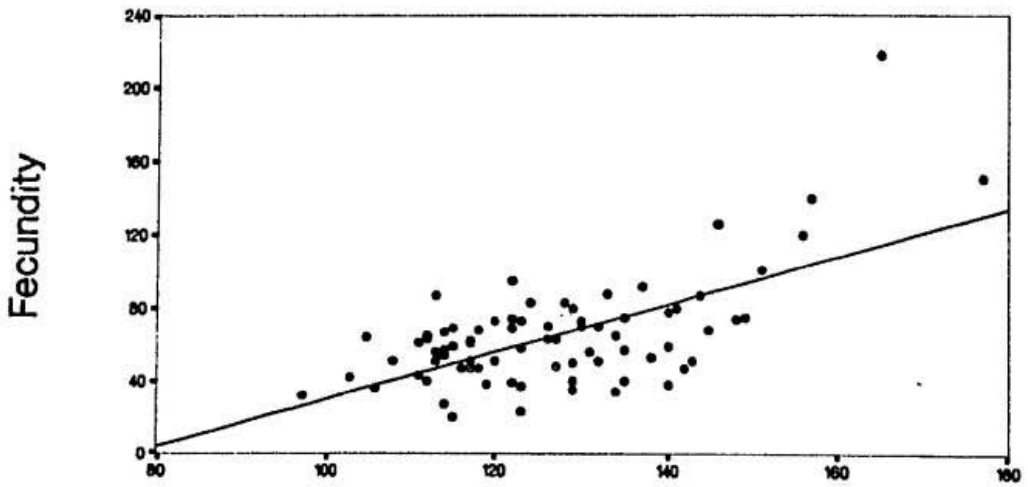


FIGURE 11. Relationship between fecundity and maternal length in Cripple Cove and Watern Cove populations. (Note: axes at different scales.)

Cripple Cove



Watern Cove



River can be expected to produce 15 to 53% more eggs than similarly sized females from the other three populations (Table 19).

Egg size was positively correlated with female length in each of the four populations (Table 18). Significant slope heterogeneity existed among the four egg size-body length regressions ($F=5.51$; $p=0.0011$; Figs. 12,13,14). When the population having the lowest slope (Cripple Cove) was excluded from the analysis (Table 18), the regression slopes were homogeneous among the three remaining populations ($F=2.86$; $p=0.06$) although the intercepts were different ($F=18.66$; $p=0.0001$). Standardized egg diameter differed by 0.98 mm among populations, with Freshwater females producing the largest eggs and Cripple Cove females producing the smallest eggs (Table 19). In terms of egg volume (an appropriate measure of egg energy content [Wootton and Evans, 1976]), a 122 mm long female from Freshwater can be expected to produce eggs that are more than twice the volume of those produced by a similarly sized female from Cripple Cove (egg volume was calculated from the equation $V = \pi d^3/6$ which describes the relationship between the volume of a sphere, V, and its diameter, d.)

FIGURE 12. Linear regressions relating egg size to maternal length in four brook trout populations on Cape Race.

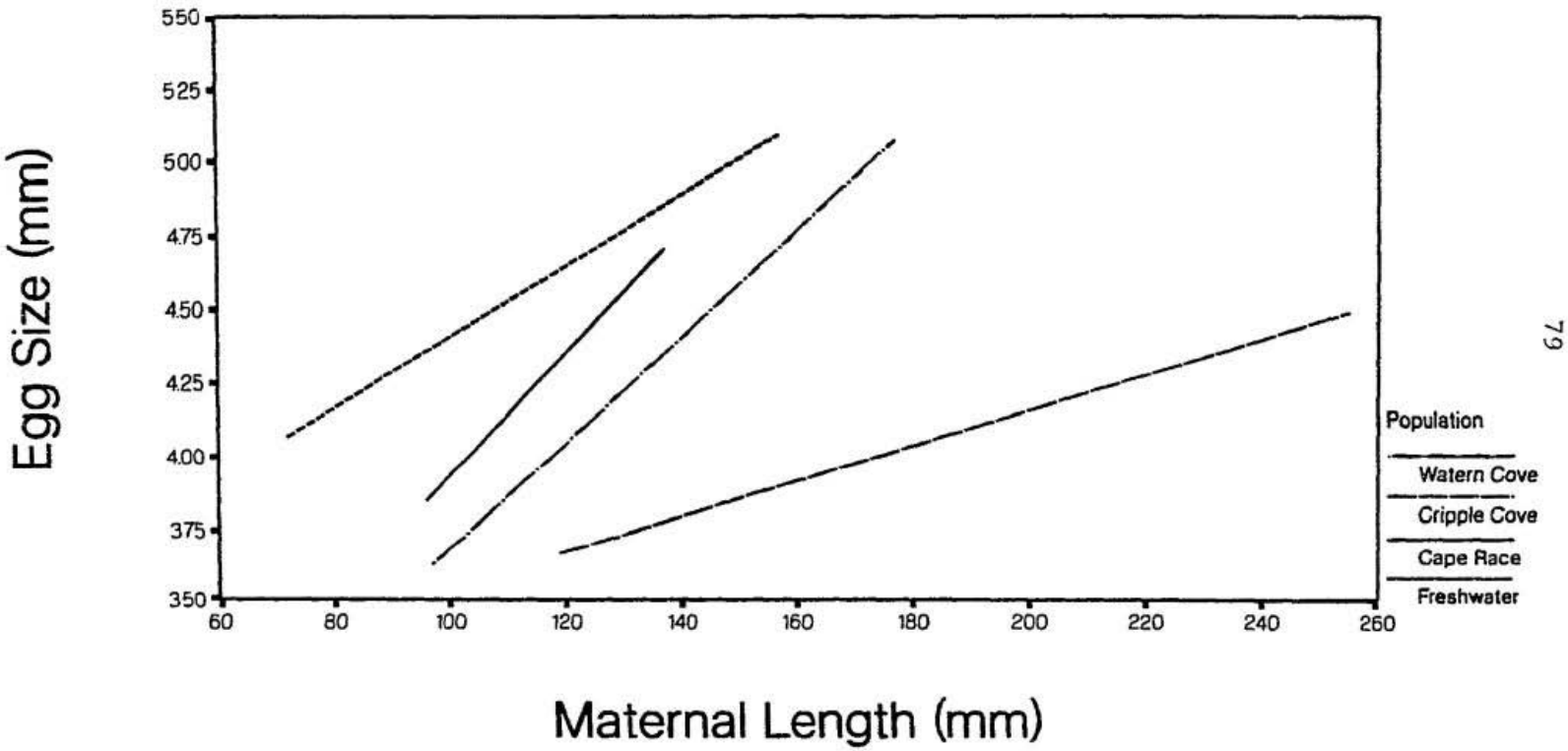
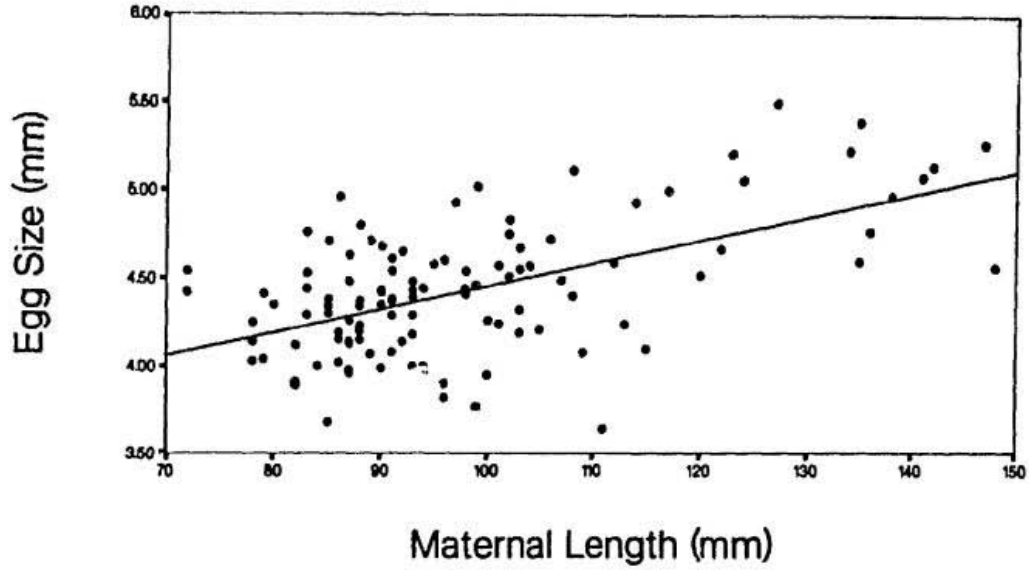

Egg Size (mm)
550
525
500
475
450
425
400
375
350
60
80
100
120
140
160
180
200
220
240
260
Maternal Length (mm)
Population
Watern Cove
Cripple Cove
Cape Race
Freshwater

FIGURE 13. Relationship between egg size and maternal length in Freshwater and Cape Race populations. (Note: axes at different scales.)

Freshwater



Cape Race

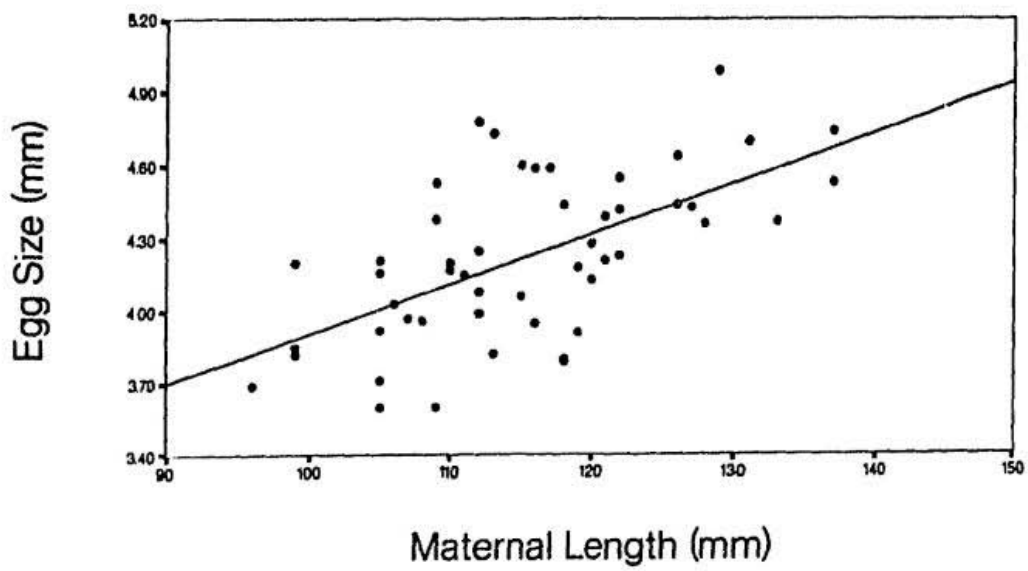
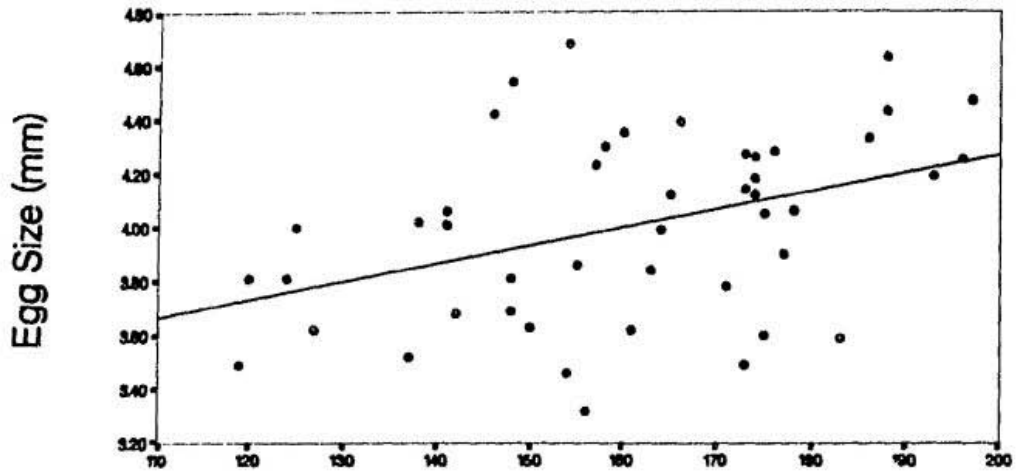
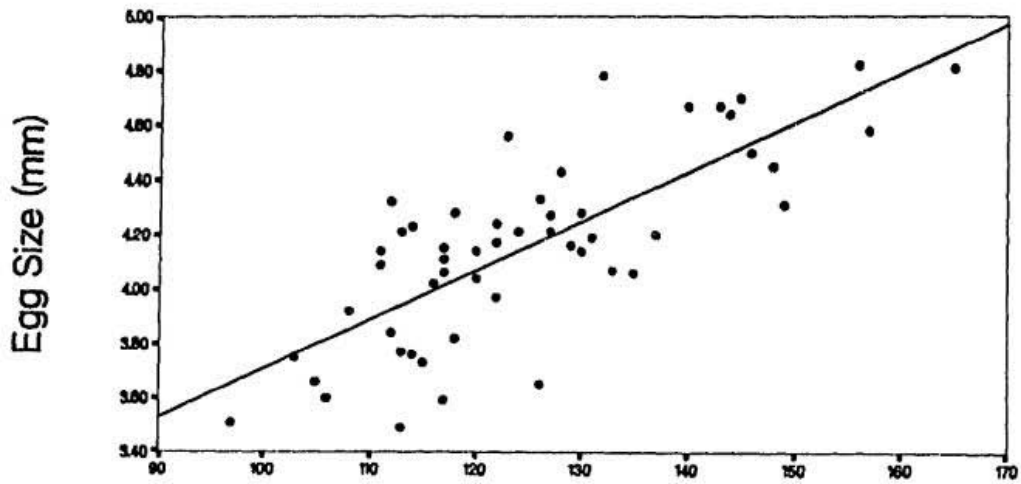


FIGURE 14. Relationship between egg size and maternal length in Cripple Cove and Watern Cove populations. (Note: axes at different scales.)

Cripple Cove



Watern Cove



3.5.3 Trade-Off Between Egg Size and Egg Number

There was a trade-off between egg size and egg number within each of the four populations. Partial correlation coefficients between egg size and egg number (controlling for gonad weight) were negative in Freshwater (-0.75, $p<0.001$, n=55), Cape Race (-0.74; $p<0.001$, n=47), Cripple Cove (-0.60, $p<0.001$, n=45), and Watern Cove (-0.68, $p<0.001$, n=49) populations. To determine whether the trade-off between egg number and egg size differed qualitatively among populations, I first multiplied egg number by mean egg volume for each female. Then, I regressed this product against gonad weight for each population and compared the slopes of the regressions using an ANCOVA (Table 21). To control partially for potential parity effects, I restricted the analysis to individuals in the youngest and second youngest age classes of mature females in each population. The slopes did not differ significantly among populations ($F=1.57$; $p=0.20$). This indicated that the rate of increase in reproductive biomass with gonad weight was equal among populations. There were significant differences in the intercepts among populations ($F=408.37$; $p<0.001$).

Expected fecundities for eggs of different sizes were calculated from multiple regression equations which described fecundity (y) as a function of gonad weight in

TABLE 21. Parameter estimates (slope and intercept) and R^2 for linear regressions relating reproductive biomass (egg number x egg volume) to gonad weight for four Cape Race brook trout populations.

Population	Slope	Intercept	R^2
Freshwater	1037	-107	0.92
Cape Race	944	- 55	0.90
Cripple Cove	1027	-533	0.94
Watern Cove	903	-103	0.88

grams (x) and egg volume in mm^3 (z) (with potential parity effects controlled - see above):

Freshwater:	$y = 17.7x - 0.62z + 33.3$	(n=108, r=0.92)
Cape Race:	$y = 17.9x - 0.74z + 41.5$	(n= 47, r=0.90)
Cripple Cove:	$y = 28.3x - 2.66z + 83.6$	(n= 45, r=0.96)
Watern Cove:	$y = 22.6x - 1.00z + 39.8$	(n= 49, r=0.90) .

One example of the trade-off between egg number and egg size is illustrated for the Watern Cove population in Fig. 15.

3.6 Brook Trout Survival Probabilities

3.6.1 Age-Specific Survival (Static Life Table Analysis)

Static life tables for each of the four populations are presented in Table 22. Because ages 1 through 6 represent individual ages at reproduction, the ages of individuals collected in June reflect the fact that these fish have lived 67% of their current year of life.

All age-specific survival probabilities have been expressed as the probability of surviving from age=1.67 to the age of interest. (Fish in their first year of life could not be reliably sampled because of their small size and were excluded from the analysis.) The numbers of individuals in each age class were standardized such that

FIGURE 15. Trade-off between egg size and egg number for a series of gonad weights for brook trout in Watern Cove river.

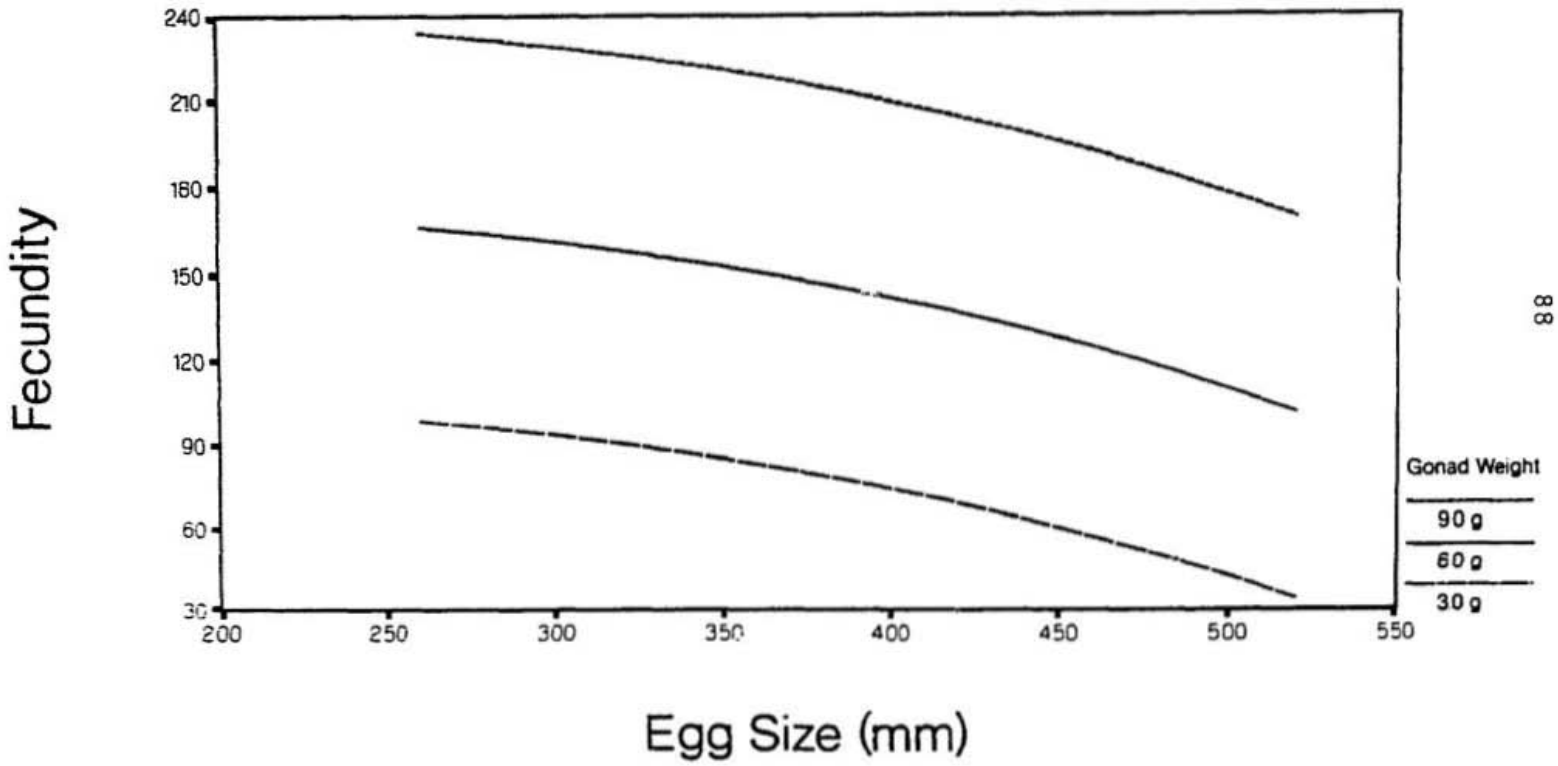

Fecundity
240
210
180
150
120
90
60
30
200
250
300
350
400
450
500
550
Egg Size (mm)
Gonad Weight
90 g
60 g
30 g

TABLE 22. Static life tables for Freshwater, Cape Race, Cripple Cove, and Watern Cove populations (values of a_x for ages 2,3,4,5 and 6 were determined from Fig. 16).

Population	Age (x)	Number alive at age x (n_x)	Standardized number alive at age x (a_x)	Probability of surviving from age=1.67 to x (l_x)
Freshwater	1.67	157	1000	----
	2.67	74	471	0.47
	3.67	57	363	0.36
	4.67	9	57	0.06
	5.67	2	13	0.01
	6.67	0	0	0
	2	-	851	0.85
	3	-	398	0.40
	4	-	151	0.15
	5	-	40	0.04
	6	-	7	0.01
Cape Race	1.67	127	1000	----
	2.67	71	559	0.56
	3.67	11	86	0.09
	4.67	1	8	0.01
	5.67	0	0	0
	2	-	794	0.79
	3	-	245	0.24
	4	-	52	0.05
	5	-	6	0.01
Cripple Cove	1.67	155	1000	----
	2.67	76	490	0.49
	3.67	28	181	0.18
	4.67	10	64	0.06
	5.67	2	13	0.01
	6.67	0	0	0
	2	-	813	0.81
	3	-	355	0.35
	4	-	132	0.13
	5	-	38	0.04
	6	-	6	0.01

Table 22 (cont'd)

Population	Age (x)	Number alive at age x (n_x)	Standardized number alive at age x (a_x)	Probability of surviving from age=1.67 to x (l_x)
Watern Cove	1.67	177	1000	----
	2.67	119	672	0.67
	3.67	78	441	0.44
	4.67	17	96	0.10
	5.67	3	17	0.02
	6.67	0	0	0
	2	-	891	0.89
	3	-	513	0.51
	4	-	219	0.22
	5	-	60	0.06
	6	-	7	0.01

1000 individuals of age=1.67 were alive in each population. These values were $\log_{(10)}$-transformed and plotted against age. Age-specific survival probabilities to reproduction (i.e., age classes 2,3,4,5, and 6) were then determined from these semi-logarithmic survivorship curves that were fitted by eye (Figure 16). Survivorship differed significantly among the four populations. With two exceptions, age-specific survival from ages 2 to 5 were significantly different among populations (l_2: G=41.92, $X^2_{0.05[3]}$=7.81; l_3: G=159.09; l_4: G=128.62; l_5: G=53.89). The exceptions were l_2 between Cape Race and Cripple Cove populations (G=1.14; $X^2_{0.05[1]}$=3.84), and l_4 and l_5 between Freshwater and Cripple Cove populations (G=1.49 and 0.05, respectively). Age class 6 was represented in Freshwater, Cripple Cove, and Watern Cove populations and there were no significant differences in the l_6 values among these 3 populations (G=0.11; $X^2_{0.05[2]}$=5.99).

3.6.2 Post-Reproductive, Overwinter Mortality

There were significant differences in post-reproductive, overwinter mortality among Freshwater, Cape Race, Cripple Cove, and Watern Cove populations (Table 23). The survival of mature females in Freshwater was significantly less than that for females from the other three populations (comparison of numbers of marked

FIGURE 16. Survivorship curves (June) for brook trout in four Cape Race populations.

Cripple Cove
log(lx)
Age (yr)
Watern Cove
log(lx)
Age (yr)
Freshwater
log(lx)
Age (yr)
Cape Race
log(lx)
Age (yr)

Table 23. Size (mean ± s.d.) and numbers of immature and mature male and female brook trout collected in the autumn and spring samples from four Cape Race rivers (M=mature male; F=mature female; I=immature males and females).

Population	Sex	Season	Length (mm)	Sample Size	Overwinter Survival
Freshwater	M	Autumn	101.5 ± 17.5	95	
		Spring	94.6 ± 13.7	11	0.12
	F	Autumn	105.5 ± 17.5	181	
		Spring	96.4 ± 9.8	21	0.12
	I	Autumn	65.1 ± 12.0	41	
		Spring	78.9 ± 17.1	672	
Cape Race	M	Autumn	126.6 ± 18.4	80	
		Spring	125.8 ± 15.9	17	0.21
	F	Autumn	118.6 ± 13.7	97	
		Spring	117.7 ± 10.6	30	0.31
	I	Autumn	78.7 ± 17.1	176	
		Spring	87.4 ± 23.1	373	

Table 23 (cont'd)

Population	Sex	Season	Length (mm)	Sample Size	Overwinter Survival
Cripple Cove	M	Autumn	155.8 ± 23.4	125	
		Spring	155.8 ± 16.9	29	0.23
	F	Autumn	153.7 ± 24.6	46	
		Spring	158.9 ± 22.7	18	0.39
	I	Autumn	95.2 ± 26.5	717	
		Spring	95.9 ± 28.4	762	
Watern Cove	M	Autumn	133.2 ± 20.3	89	
		Spring	130.3 ± 24.4	28	0.31
	F	Autumn	124.8 ± 13.2	166	
		Spring	126.1 ± 12.6	59	0.36
	I	Autumn	80.3 ± 20.8	722	
		Spring	104.8 ± 25.4	1045	

individuals alive and presumed dead in the spring among four populations: G=23.84, $X^2_{0.05[3]}$=7.81; three populations: among three populations: G=0.75, $X^2_{0.05[2]}$=5.99). Male survival differed significantly among the four populations (G=11.33; $X^2_{0.05[3]}$=7.81) although these significant differences disappeared when either Freshwater or Watern Cove population was removed from the analysis. There were no significant differences in overwinter survival between sexes within any of the populations.

Body size influenced post-reproductive, overwinter survival within populations (Table 24). There were significant differences in survival among four size classes for mature females in Freshwater (G=11.24) and for mature males in Cripple Cove (G=8.76) (Table 25). Survival was 9% (Cape Race females) to 47% (Freshwater females) lower in the smallest size class relative to the next largest size class for both sexes in all populations (with the exception of Freshwater males).

3.6.3 Age-Specific Overwinter Survival Probabilities for Mature and Immature Individuals

The indirect calculations of age for mature and immature fish collected in October, 1988, were based on the significant positive correlations between age and length (cf. Table 17). First, the lengths of fish of known age

Table 24. Size frequencies of marked and recaptured brook trout from four Cape Race populations (N_m=number of fish marked in the autumn; N_r=number of marked fish recaptured the following spring).

Sex	Length midpoint (mm)	Population: Freshwater N_m	Freshwater N_r	Cape Race N_m	Cape Race N_r	Cripple Cove N_m	Cripple Cove N_r	Watern Cove N_m	Watern Cove N_r
Fem	80	26	3	0	0	0	0	0	0
	100	92	15	28	8	0	0	0	0
	120	46	3	56	18	3	0	18	4
	140	12	0	12	4	19	7	91	35
	160	4	0	1	0	17	9	52	17
	180	1	0	0	0	5	0	4	3
	200	0	0	0	0	1	1	0	0
	220	0	0	0	0	1	1	1	0
	240	0	0	0	0	0	0	0	0
Male	80	23	4	0	0	0	0	0	0
	100	49	6	16	3	0	0	6	4
	120	18	1	31	7	8	0	39	11
	140	3	0	25	7	55	13	30	10
	160	1	0	6	0	31	13	10	2
	180	1	0	1	0	17	1	3	0
	200	0	0	1	0	10	2	0	0
	220	0	0	0	0	3	0	1	1
	240	0	0	0	0	1	0	0	0

Table 25. Size-specific overwinter survival probabilities for mature female and male brook trout from four Cape Race populations (length classes in which the number of marked individuals was less than 10 were excluded).

Sex	Length midpoint (mm)	Population			
		Freshwater	Cape Race	Cripple Cove	Waterl. Cove
Fem	80	0.12	-	-	-
	100	0.16	0.29	-	-
	120	0.07	0.32	-	0.22
	140	0	0.33	0.37	0.38
	160	-	-	0.53	0.33
Male	80	-	-	-	-
	100	0.17	0.19	-	-
	120	0.12	0.23	-	0.28
	140	0.06	0.28	0.24	0.33
	160	-	-	0.42	0.20
	180	-	-	0.06	-
	200	-	-	0.20	-

collected from each of the four populations in June, 1988, were extrapolated to obtain expected age-specific lengths in October. The October lengths were calculated using the equation

$$L_{Oi} = L_{Ji} + (\tau_i \times 0.8) , \qquad (1)$$

where L_{Oi} and L_{Ji} represent the lengths of fish in October and June, respectively, τ_i is the annual increase in length of fish of age i, and 0.8 is a constant which reflects the expected increase in length of a fish from June to October. The calculation of this constant was based on three assumptions: (1) growth is restricted to five months (May through September), (2) growth is approximately linear throughout the growing months (cf. Fig. 2) and (3) field data represent growth rather than differential mortality. Consequently, a fish will attain 80% of its annual growth between June and October. Expected annual growth increments are the differences in mean length between successive ages in the June samples. The extrapolated length data for the October sample are presented in Table 26.

Mature and immature fish collected in the autumn were aged according to the age class in which their lengths were grouped (Table 27). The lengths included in each class encompassed the 68% confidence interval, i.e., a 1 standard

Table 26. Expected mean age-specific lengths (mm) of brook trout in October, based on June length-age data (1 s.d. length range in parentheses).

Population	Age (years) 2	3	4	5
Freshwater	79.2 (73-85)	93.6 (88-99)	107.8 (102-114)	138.5 (132-151)
Cape Race	109.9 (103-117)	130.1 (123-137)	154.7 (145-164)	
Cripple Cove	104.8 (96-114)	133.8 (125-143)	160.2 (151-169)	179.5 (172-186)
Watern Cove	100.7 (93-108)	125.3 (117-133)	145.2 (137-153)	173.3 (165-181)

Table 27. Age-specific frequencies of brook trout in the autumn and spring collections from four Cape Race rivers.

Population	Sex	Season	Age (years) 2	3	4
Freshwater	M	Autumn	14	30	23
		Spring	3	2	3
	F	Autumn	19	67	57
		Spring	3	12	6
	Mature	Autumn	33	97	80
		Spring	6	14	10
	Immature	Autumn	108	14	0
		Spring	194	144	41
Cape Race	M	Autumn	18	28	0
		Spring	5	4	0
	F	Autumn	29	37	0
		Spring	8	7	0
	Mature	Autumn	47	65	0
		Spring	13	11	0
	Immature	Autumn	13	0	0
		Spring	62	23	0
Cripple Cove	M	Autumn	1	44	30
		Spring	0	11	13
	F	Autumn	0	14	23
		Spring	0	5	8
	Mature	Autumn	1	58	53
		Spring	0	16	21
	Immature	Autumn	233	87	2
		Spring	182	112	19

Table 27 (cont'd).

Population	Sex	Season	Age (years) 2	3	4
Watern Cove	M	Autumn	4	28	21
		Spring	3	10	7
	F	Autumn	14	85	37
		Spring	4	29	15
	Mature	Autumn	18	113	58
		Spring	7	39	22
	Immature	Autumn	175	36	0
		Spring	274	249	76

deviation range on either side of the mean. This confidence interval was chosen because the lengths of successive ages did not overlap. This reduced the probability of incorrectly assigning fish of a given length to any age group.

A proportion of the unmarked individuals collected in the spring were fish that had matured the previous autumn but were not collected in the autumn sample. To determine the probability that an unmarked spring fish was previously mature and to include the effect that age has on maturity, I calculated the probabilities of (1) maturity for a fish of age x (α_x), and of (2) overwinter survival for a mature fish of age x (δ_x). The number of individuals in each age group in the autumn and spring samples was used to calculate these age-specific probabilities. The age-specific probabilities of prior maturity among the unmarked individuals in the spring samples were, then, equal to $\alpha_x\delta_x$ (Table 28). The estimated number of immature fish in each age class in the spring samples of unmarked fish was calculated using the equation

$$I_x = U_x - (U_x)(\alpha_x\delta_x) \quad , \qquad (2)$$

where I_x and U_x are the theoretical and field estimates for immature fish of age x, respectively, in the spring sample.

Table 28. Age-specific probabilities of maturity and overwinter survival for four populations of brook trout on Cape Race.

Population	Age	Probability of Maturity (α)	Overwinter Survival of Mature Fish (δ)	Probability of Prior Maturity ($\alpha\delta$)
Freshwater	2	0.23	0.18	0.04
	3	0.87	0.14	0.12
	4	1.00	0.12	0.12
Cape Race	2	0.78	0.28	0.22
	3	1.00	0.17	0.17
Cripple Cove	2	0.004	0	0
	3	0.40	0.27	0.11
	4	0.96	0.40	0.38
Watern Cove	2	0.09	0.39	0.04
	3	0.76	0.34	0.26
	4	1.00	0.38	0.38

3.6.4 The Influence of Maturity on Overwinter Survival

The influence of maturity on overwinter survival was examined by comparing the relative survival of mature and immature individuals. Survival probabilities were calculated separately for mature and immature fish, using the equation

$$s_i = (n_i x_i)/\Sigma n_i x_i \ , \qquad (3)$$

where s_i represents the relative proportion of age i in the spring, n_i is the number of individuals of age i in the autumn (numbers were standardized such that $n_2 + n_3 + n_4 = 100$), and x_i represents the survival probability from autumn to spring of individuals of age i. To calculate age-specific survival probabilities, equation (3) becomes

$$x_i = (\Sigma n_i x_i)\ (s_i/n_i)$$
$$x_i = (s_i/n_i)(k) \ . \qquad (4)$$

Since k is a constant, solving for x_i gives relative survival probabilities for mature and immature fish of age i. In using these equations, I assumed that any sampling biases were constant between the autumn and spring collection periods. To exclude values of s and r that were based on sample sizes of less than 10, males and females

were pooled for the probability calculations for mature fish (cf. Table 27). To facilitate comparisons among populations, the influence of maturity on overwinter survival was assessed by comparing the overwinter survival of mature and immature age=3 individuals among Freshwater, Cripple Cove, and Watern Cove populations (there were insufficient data to include the Cape Race population).

The results show that maturity influenced the probability of overwinter survival. Overwinter survival probabilities were consistently higher for immature individuals than they were for mature individuals at age=3 (Table 29). The largest discrepancy in probabilities was in Freshwater (a 2.7-fold difference) and the smallest difference was in Cripple Cove (a 1.4-fold difference). There was direct qualitative evidence for high reproductive costs in Freshwater. In October, 1988, four post-reproductive females that had died recently (i.e., within hours; females were brightly coloured and there was no rigor mortis) were observed floating downstream in Freshwater River.

3.7 Effects of Egg Size on Embryonic Survival and Development

Embryonic developmental characteristics and survival probabilities of eggs hatched in the laboratory are

Table 29. Relative overwinter survival probabilities for age=3 (x_3) mature and immature brook trout from three Cape Race populations.

Population	Mature Individuals	Immature Individuals
Freshwater	0.010	0.033
Cripple Cove	0.009	0.013
Watern Cove	0.010	0.022

presented in Table 30. Mean egg size ranged from 4.12 to 5.22 mm within broods. Egg size differed significantly among broods ($p<0.001$) within populations (Freshwater: $F=134.51$; Watern Cove: $F=118.44$; Cripple Cove: $F=82.17$) but not among populations ($F=0.67$; $p=0.52$). Egg number per brood ranged from 12 to 343.

Embryonic survival did not differ significantly during any of the three developmental stages (Table 30). [These data are probably underestimates because unfertilized eggs could not be distinguished from fertilized eggs until the eyed stage of development.] Pooling data among populations, egg size was uncorrelated 1) with embryonic survival to the eyed stage ($r=-0.04$; $p=0.73$), 2) with survival from the eyed stage to hatching ($r=0.05$; $p=0.71$), and 3) with survival from hatching to yolk sac resorption ($r=-0.11$; $p=0.38$).

In all populations, egg size was positively correlated with size at hatching and size at yolk sac resorption (range in $r=0.55$-0.76). Neither size at hatching ($F=1.34$; $p=0.27$) nor size at yolk sac resorption ($F=0.08$; $p=0.92$) differed among the three populations.

Time from fertilization to hatching (developmental time) averaged 75.8 $\pm$ 2.2 days and did not differ significantly among populations ($F=1.14$; $p=0.33$). Egg size was uncorrelated with developmental time (pooled $r=-0.16$;

TABLE 30. Embryonic development and survival for three populations of brook trout (data are means with standard deviations in parentheses).

Trait	Population: Freshwater (n=15)	Cripple Cove (n=27)	Watern Cove (n=24)
Egg size (mm)	4.80 (0.33)	4.70 (0.27)	4.72 (0.30)
Egg number	47 (25)	190 (79)	55 (28)
Time to hatching (days)	75.3 (3.0)	75.8 (2.1)	76.0 (1.7)
Size at hatch (mm)	17.0 (1.5)	17.0 (1.0)	16.6 (1.2)
Size at yolk sac resorption (mm)	21.8 (1.0)	22.0 (1.9)	22.2 (1.5)
Survival (proportion)			
Pre-eyed stage	0.84 (0.08)	0.91 (0.10)	0.91 (0.08)
Eyed to hatch	0.98 (0.02)	0.96 (0.05)	0.96 (0.05)
Hatch to yolk sac resorption	0.90 (0.16)	0.98 (0.04)	0.98 (0.03)

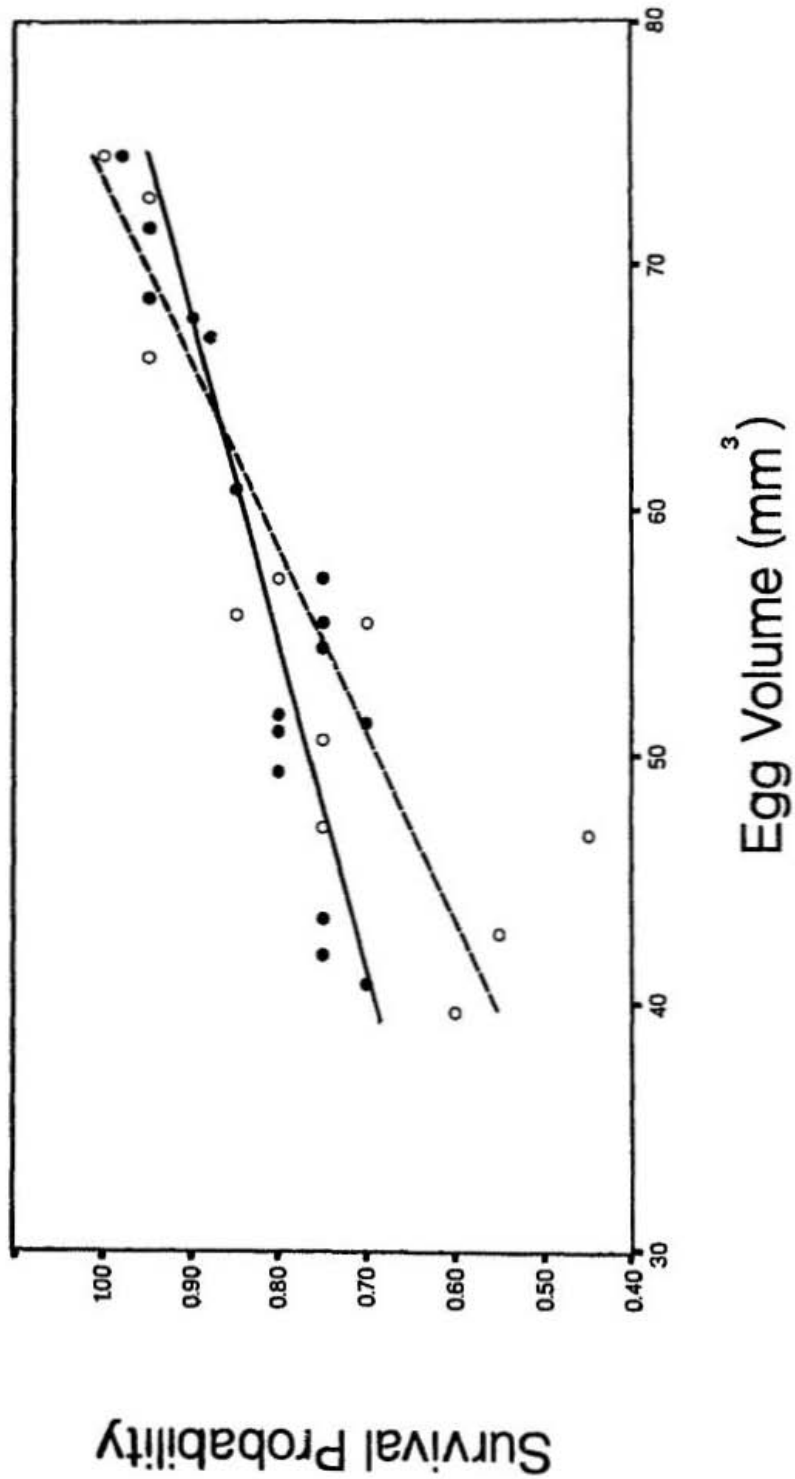
p=0.19) and accounted for no more than 7% of the variation in developmental time in any of the populations.

3.8 Effect of Egg Size and Food Supply on Juvenile Survival

Juvenile survival was positively correlated with egg size during the first 20 days of exogenous feeding at both low ($r=0.88$; $p<0.001$; n=11 broods) and high ($r=0.87$; $p<0.001$; n=16) food levels (Fig. 17). Food supply influenced the effect of egg size on juvenile survival to 20 days. The slopes of the linear regressions relating juvenile survival to egg size were not the same for the two food levels ($F=5.66$; $p=0.02$). Decreased food abundance resulted in higher mortality for the smallest egg sizes with a negligible effect on the largest sized eggs.

The influence of food supply and egg size on juvenile survival was strongest during the first 20 days of exogenous feeding. Juvenile survival to 50 days was positively correlated with egg size at both low ($r=0.81$; $p=0.001$; n=8 families) and high ($r=0.77$; $p=0.001$; n=13) food levels. However, the slopes of the regressions relating juvenile survival to egg size were not significantly different at the two food levels ($F=2.01$; $p=0.17$), nor were they significantly different between the 20 and 50 day survival probabilities within each ration (low ration: $F=0.02$, $p=0.89$; high ration: $F=0.17$, $p=0.68$). This lack of slope

FIGURE 17. Relationship between juvenile survival at 20 days and egg size at high (closed circles) and low (open circles) levels of food. Data points correspond to broods reared in separate aquaria.


Survival Probability
1.00
0.90
0.80
0.70
0.60
0.50
0.40
30
40
50
60
70
80
Egg Volume (mm³)

heterogeneity - despite their similar correlation coefficients - can be attributed to the smaller sample sizes at the 50 day time period (a technical failure in the air supply resulted in the death of several fish in six broods 28 days after the beginning of the experiment). Survival within each of the time intervals examined after the first 20 days (i.e., 21-30, 31-40, and 41-50 days following yolk sac resorption) was independent of ration level ($p>0.05$) and of egg size (r^2 less than 1% for data pooled from both ration levels for each of the time intervals). Daily mortalities occurring during the first 50 days of exogenous feeding were always incurred by the smallest or next to smallest sibling within each brood.

The experiment with four replicates from a single brood showed that tank effects did not contribute to variation in juvenile survival ($G=0.43$, 3 d.f., $p>0.10$). At 20 days post-yolk sac resorption, two fish had died in two of the tanks, and three fish had died in each of the other two tanks.

3.9 Interactive Effects of Egg Size and Food Supply on Maternal Fitness

Maternal fitness per brood can be approximated by

$$w_{ijk} = (m_{ij})(l_{ik}) \qquad (5)$$

where m_{ij} is the expected number of eggs of size i that can be produced in a gonad of weight j, l_{ik} is the survival probability of eggs of size i in environment k (i.e., environments differing in food supply), and w_{ijk} represents the fitness of females producing eggs of size i, in a gonad of weight j, in environment k.

I considered fecundity to be primarily a function of egg size and gonad weight. There was empirical evidence of a trade-off between egg size and egg number in each of the Cape Race populations (cf. section 3.5.3). The observed trade-off between egg number and egg size was independent of gonad weight and did not differ among populations. Consequently, expected numbers of eggs for a given combination of egg size and gonad weight were calculated using empirical data from only one population (Cripple Cove). These data were determined from the multiple regression equation which relates fecundity (y) to gonad weight (x) and egg volume (z), i.e. $y = 28.3x - 2.66z + 83.6$.

Juvenile survival probabilities (l_{ik}) were calculated from the linear regression equations that related probability of survival to the twentieth day of exogenous feeding in environment k, l_k, to egg volume (mm^3), i, for low (k=1) and high (k=2) food levels. These were

$$l_1 = 0.013i + 0.026 \quad (6)$$

$$l_2 = 0.008i + 0.378 \quad (7)$$

where (6) and (7) were the regression equations that were determined experimentally for the low and high food levels, respectively (cf. Fig. 17).

The fitness consequences of producing eggs of a given size varied with food supply within each population (e.g. Cripple Cove: Fig. 18). The egg size that maximized number of surviving offspring (i.e., the optimal egg size) increased as food supply decreased (Table 31). Optimal egg sizes for low and high food levels ranged 0.7 to 0.9 mm in diameter. Thus, maximum maternal fitness is achieved through the production of small eggs when food supply is high and through the production of large eggs when food supply is low.

3.10 Evolutionarily Stable Strategies of Age at Maturation

If the observed ages at maturation and indices of reproductive effort are evolutionarily stable, then the present strategies should be such that they maximize fitness. It is generally agreed that the most appropriate measure of fitness in a density-independent environment is the intrinsic rate of natural increase, r, which is given by

FIGURE 18. Calculated relationship between egg size and maternal fitness at two levels of juvenile food abundance.

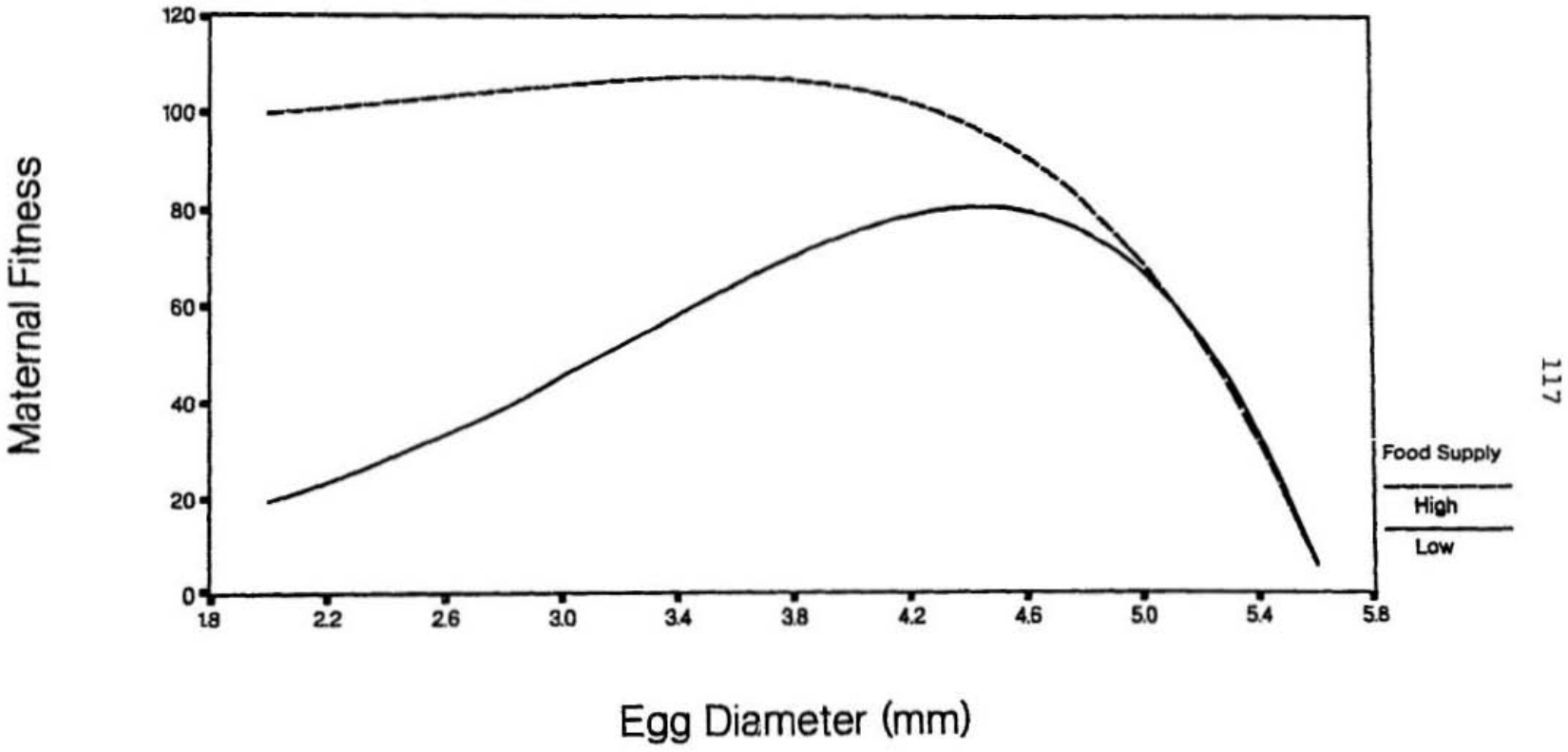

Maternal Fitness
120
100
80
60
40
20
0
1.8
2.2
2.6
3.0
3.4
3.8
4.2
4.6
5.0
5.4
5.8
Egg Diameter (mm)
Food Supply
High
Low

Table 31. Predicted optimum egg sizes (mm) in two environments differing in food abundance for three brook trout populations.

	Food Abundance	
Population	Low	High
Freshwater	4.7	4.0
Cripple Cove	4.5	3.6
Watern Cove	4.7	3.9

the discrete-time version of the Euler-Lotka equation (Taylor et al., 1974; Charlesworth, 1980)

$$\Sigma\, e^{-rx}\, l_x\, m_x = 1 \quad . \qquad (9)$$

The probability of a female surviving from fertilization to the beginning of the breeding season when she is of age x is designated l_x. The expected number of zygotes produced by a female of age x is represented by m_x.

As in many organisms having indeterminant growth, age-specific rates in fish are best expressed in terms of body size, a character that is correlated with most life history traits in salmonid fish (Hutchings and Morris, 1985). Furthermore, the lengths of post-reproductive females should reflect the reduction in growth that is concomitant with maturation in salmonids (Myers et al., 1986; Rowe and Thorpe, 1990). I quantified female length at any age x in relation to the mean length of immature females at age=2, this being the last age at which present or prior maturity is reliably known. The lengths of age=2 immature fish in each population were taken to be those lengths less than the 95% confidence limit of the mean length of mature age=3 fish but greater than the maximum length of age=1 fish (whose age can be reliably assessed by body size). The mean lengths of age=2 immature females are presented in Table 32.

Table 32. Length ranges and mean lengths of immature age=2 brook trout in four Cape Race populations.

Population	Upper 95% confidence limit for age=1 fish (mm)	Lower 95% confidence limit for age=3 fish (mm)	Mean length of immature age=2 fish (mm)
Freshwater	63	81	73.4
Cape Race	75	107	78.0
Cripple Cove	73	114	77.1
Watern Cove	70	113	75.3

Age-specific lengths for immature fish, for females maturing for the first time, and for previously mature females are given, respectively, by the equations

$$s_i = s_2 + d_{i,2} \qquad (i>1) \ , \qquad (10)$$

$$S_\alpha = (s_2 + d_{\alpha,2})(1-\phi) \qquad , \qquad (11)$$

$$S_{i+\alpha} = S_\alpha + D_{i+\alpha,\alpha} \qquad (i\geq 1) \ , \qquad (12)$$

where s_i represents the length of immature females of age i, $S_{i+\alpha}$ represents the length of previously mature females of age $i+\alpha$, and α is age at first reproduction. Mean length differences between age classes are denoted by d and D for immature and mature females, respectively. The reduction in length resulting from maturation is denoted by ϕ at the age of first reproduction. A value of 0.04 was used for ϕ in this study. This value was based on the mean 4% reduction in growth documented for male Atlantic salmon parr that matured at a size similar to that of female brook trout on Cape Race (Myers et al., 1986). Length differences between successive age classes of mature females were those recorded from the October, 1987-88, field data (Table 33). Length differences between successive age classes of immature fish were those recorded in the June, 1988, collections (cf. Table 16). Thus, if a female matured at age=2, then her length was the mean length of immature age=2 fish less 4 per cent. Her lengths at successive ages (assuming annual

Table 33. Length (mm) at age for mature female brook trout in four Cape Race rivers. Data are means and standard deviations with sample sizes in parentheses.

	Age (years)				
Population	2	3	4	5	6
Freshwater	81.1 4.5 (18)	91.1 4.9 (55)	112.2 12.7 (34)	136.6 22.3 (8)	
Cape Race	106.3 4.9 (20)	120.9 7.0 (29)	133.0 - (1)		
Cripple Cove	119.0 - (1)	128.5 7.3 (6)	152.3 7.2 (18)	176.1 7.7 (21)	193.0 6.1 (3)
Watern Cove	109.8 5.0 (15)	122.3 4.7 (21)	137.3 6.8 (10)	150.2 5.9 (5)	165.0 - (1)

reproduction among previously mature females) were equal to her length at age=2 plus the length difference between the appropriate ages of mature females. At age of first reproduction, α, length was equal to the length in the previous age class plus the length difference between successive ages for immature fish less 4 per cent.

Annual survival for any fish was divided into a summer (June-September) period and an overwinter (October-May) period. Age-specific survival was determined from the equation

$$l_x = \delta(l_w)(l_s) \quad , \qquad (13)$$

where l_w and l_s denote overwinter and summer survival probabilities, respectively, and δ is a parameter that reflects the differential probability of overwinter survival between immature and mature fish. For immature fish, δ is equal to the relative survival of immature fish divided by the relative survival of mature fish (cf. Table 29). For mature fish, δ equals 1. Overwinter survival probability for mature fish was equal to the mean overwinter survival calculated empirically for each population from the 1988-1989 samples (cf. Table 23). Summer survival probability for each population was calculated from the static life tables as the probability of surviving from age=1.67 (i.e., June) to age=2.00 (i.e., October) (cf. Table 22).

Overwinter and summer survival probabilities were calculated independently of age because of insufficient sample sizes (Table 34).

The expected number of female zygotes (i.e., eggs) produced by a female of age x is

$$m_x = \theta(S_x) + \epsilon \quad , \qquad (14)$$

where S_x is the size of a mature female of age x, and θ and ϵ represent the slope and intercept, respectively, of the regressions relating fecundity to body size for each population (cf. Table 18). Ages at first reproduction were simulated for ages 2 to 5, as observed in each population. Reproduction was assumed to occur annually.

The Euler-Lotka equation (9) is usually used to measure the rate of increase of an entire population. I use it here to assess the rate of increase of the population of individuals having a specific reproductive phenotype. Thus, following Sibly and Calow (1983: 529) and Charlesworth, 1980: 231), the fitness of phenotype p in a specific environment can be measured by the rate of increase $r(p)=r^*$ defined by the equation

$$\sum_x e^{-r^*x} l_x(p)\, m_x(p) = 1 \quad . \qquad (15)$$

Table 34. Summer and winter survival probabilities for immature and mature brook trout in four Cape Race populations.

	Survival Probability		
	Summer	Winter	
Population		Immature	Mature
Freshwater	0.85	0.40	0.12
Cape Race	0.79	-[A]	0.31
Cripple Cove	0.81	0.56	0.39
Watern Cove	0.89	0.72	0.36

[A] insufficient data

Sibly and Calow (1983: 545-546) have shown that fitness can be defined in this way for both density-independent and density-dependent environments. Age-specific fecundity, m_x, is the variable to which equation (15) is most sensitive. Of all the variables used directly or indirectly in this equation, m_x is probably the most accurate one because it is based on highly significant length-age and fecundity-length regressions.

The results indicate that there was strong selection for females in Freshwater to mature at the earliest age possible. Maximum fitness was achieved when females matured at age=2 and reproduced annually thereafter (Table 35). For Watern Cove females, fitness was maximized when maturation was postponed to age=3. Fitness was maximized in the Cripple Cove population when females matured initially at either ages 3 or 4.

Table 35. Modified intrinsic rate of increase (r^*) for different ages at first reproduction (α) for female brook trout in three Cape Race populations.

Population	α	r^*
Freshwater	2	1.10
	3	0.77
	4	0.40
	5	0.12
Cripple Cove	2	0.24
	3	0.78
	4	0.73
	5	0.54
Watern Cove	2	0.54
	3	1.05
	4	0.83
	5	0.64

Chapter Four

DISCUSSION

4.1 The Scale of Life History Variation in Brook Trout

4.1.1 Large- Versus Small-Scale Variation

The significance of the life history variation at Cape Race must be assessed within the scope of life history variation throughout the geographical range of the brook trout. The endemic range of this species includes northeastern North America from Ungava Bay south to Cape Cod, a narrow intrusion southward into Georgia along the Appalachian Mountains, west in the upper Mississippi and Great Lakes drainages to Minnesota, and north to Hudson Bay (Scott and Crossman, 1973).

I collated population data on growth rate, size at maturity, fecundity and egg size from the literature to compare small- and large-scale variation in brook trout life history. Differences in growth rate were approximated as differences in body length (both sexes combined) in the third year of life. Fecundity - maternal length linear regressions were estimated from published empirical data, regression lines, or age- and size-specific fecundities. Published accounts of egg size variation were few, the most

extensive data set being from Cape Race. Egg size data were not included if the fish were sampled more than 1 month prior to expected spawning time. Linear regressions between egg size and maternal length were calculated from empirical data (present study; Verreault and Langlois, 1984), least squares regression line (Wydoski and Cooper, 1966), and both length-specific (Vladykov, 1956) and age-specific egg sizes (Johnston and McKenna, 1974).

The 3.4-fold difference in body size at the end of the third year of life (Freshwater River, Nfld.: 93 mm; Dickson Lake, Ont.: 313 mm) was indicative of tremendous variability in growth of this species throughout its geographical range (Table 36). Growth rates for the seven Cape Race populations were among the slowest, with the third year lengths of all but Cripple Cove being among the smallest 8 of the 35 documented populations. Length at maturity for female brook trout ranged from 72 mm (20 eggs of 4.54 mm diameter, Freshwater River, Nfld.; present study) to 559 mm (5630 eggs of unknown size, Lake Nipigon, Ont; Ricker, 1932). The smallest known mature male brook trout is 63 mm from Freshwater River, Nfld. (present study).

The rate at which fecundity increased with maternal length varied by more than one order of magnitude (Table 37). With the exception of those for Cripple Cove and Drook, the regression slopes for the Cape Race populations were the smallest. The intercepts for the Cape Race

TABLE 36. Geographical variation in brook trout growth (lengths in September/October unless indicated otherwise).

Location	Latitude (N)	Length during third year (mm)	Reference
Rocky Fork Ck., Tennesee	36° 10'	134	Whitworth & Strange (1983)
Larry's Ck., Pennsylvania	41° 00'	147	Cooper (1967)
Spring Ck., Penn.	41° 00'	243	"
Bobb's Ck., Penn.	41° 00'	141	Wydoski & Cooper (1966)
Tomtit Run, Penn.	41° 00'	132	"
Lingle Strm., Penn.	41° 00'	142	"
Cherry Ck., Penn.	41° 00'	139	"
13 streams, Ithaca, New York	42° 30'	168	Hazzard (1932)
8 streams, SW Ontario	44° 05'	162	Witzel & MacCrimmon (1983)
Lawrence Ck., Wisconsin	44° 20'	228	McFadden (1961)
Dickson L., Ont.	45° 47'	313	Fraser (1985)
Dunk R., Prince Edward Is.	46° 21'	203	Johnston & McKenna (1974)
Watern Cove R., Newfoundland	46° 38'	123	present study
Freshwater R.,	46° 39'	93	"

Nfld.

Table 36 cont'd

Location	Latitude (N)	Length during third year (mm)	Reference
Cripple Cove R., Nfld.	46° 39'	139	present study
Cape Race R., Nfld.	46° 40'	125	"
Drook R., Nfld.	46° 40'	122	"
Wrights R., Nfld.	46° 42'	118	"
Whalens R., Nfld.	46° 42'	118	"
L. Tantaré, Québec	47° 04'	225[1]	Frenette & Dodson (1984)
Berry Hill P., Nfld.	47° 05'	148[2]	Wiseman (1969)
L. Laflamme, Qué.	47° 19'	203	Verreault & Langlois (1984)
Stephen's P., Nfld.	47° 21'	166[3]	Wiseman (1969)
Thomas' P., Nfld.	47° 21'	195[4]	"
Angle P., Nfld.	47° 24'	192[4]	"
Highlands R., Nfld.	48° 11'	160	Gibson et al. (1987)
Indian Big Bay P., Nfld.	49° 04'	189[4]	Wiseman (1969)
Big Bear Cave P., Nfld.	49° 04'	173[4]	"

TABLE 36. cont'd

Location	Latitude (N)	Length during third year (mm)	Reference
Indian R., Nfld.	49° 27'	129[2]	Wiseman (1969)
6 Gros Morne L., Nfld.	49° 37'	208[1]	Ryan & Kerekes (1988)
Matamek L., Qué.	50° 22'	112	Saunders & Power (1970)
Valley R., Labrador	53° 45'	157[2]	Wheeler (1977)
L. Laisse, Qué.	56° 15'	164	Dutil (1976)
Hayes R., Manitoba	57° 10'	295	Doan (1948)
Koksoak R., Qué.	58° 30'	108[3]	Coleman (1970)

[1] calculated length at third scale annulus
[2] length on or about August 1
[3] length between June and September
[4] length in June

TABLE 37. Geographical variation in the linear regressions relating fecundity (egg number per female) to maternal length (mm) in brook trout.

Location	Slope	Intercept	Length range of mature females (mm)	Reference
Dickson L., Ontario	13.60	-3364	295-533	Fraser (1985)
Dunk R., P.E.I.	8.36	-1234	164-393	Johnston & McKenna (1974)
Guillaum-Delisle, Québec	8.32	-1633	285-380	Dutil (1976)
Mad & Nipigon Lakes, Ont.	5.11	- 561	130-559	Ricker (1932)
Pigeon R., Michigan	4.71	- 464	144-215	Cooper (1953)
Tomtit Run, Pennsylvania	4.11	- 455	101-185	Wydoski & Cooper (1966)
Lawrence Ck., Wisconsin	4.10[1]	- 388	105-127	McFadden (1961)
Valley R., Labrador	4.03	- 406	115-235	Wheeler (1977)
Beaver P., Wyoming	3.34[1]	- 286	124-198	Allen (1956)
Koksoak R., Québec	3.18	- 443	145-500	Coleman (1970)
Cripple Cove, Newfoundland	2.66	- 281	119-197	present study
Matamek L., Qué.	2.60	- 270	122-212	Saunders & Power (1970)
Laurentide, Qué.	2.37	- 240	145-225	Vladykov (1956)

TABLE 37. cont'd

Location	Slope	Intercept	Length range of mature females (mm)	Reference
Drook R., Nfld.	1.89	- 155	108-175	present study
L. Laflamme, Qué.	1.75	- 105	189-282	Verreault & Langlois (1984)
Watern Cove, Nfld.	1.30	- 100	97-165	present study
Freshwater R., Nfld.	1.11	- 68	72-148	"
Whalens R., Nfld.	0.90	- 54	94-144	"
Wrights R., Nfld.	0.78	- 39	101-138	"
Cape Race R., Nfld.	0.63	- 19	96-137	"

[1] introduced population

populations were either the highest or among the highest throughout the range of the species (Table 37). The higher intercepts coupled with smaller slopes are indicative of generally greater size-specific fecundities at small maternal lengths among the Cape Race populations. Mean number of eggs per female ranges from 11 (egg size=4.42 mm, 80 mm female, Freshwater River, Nfld.; present study) to 5630 (559 mm female, Lake Nipigon, Ont.; Ricker, 1932) throughout the brook trout's geographical range.

The regression slopes between egg size and maternal length ranged over 1.5 orders of magnitude among 11 populations (Table 38). Size-specific egg size were generally highest for the Cape Race populations. Mean diameter of mature brook trout eggs ranged from 2.78 mm (female length=168 mm, Dunk River, P.E.I.; Johnston and McKenna, 1974) to 5.13 mm (135 mm, Freshwater River, Nfld; present study).

In summary, the small-scale variation among the Cape Race populations is at one end of a large-scale continuum of life history variation in growth, size at maturity, fecundity and egg size. Relative to populations throughout the brook trout's geographical range, the Cape Race populations have the slowest individual growth, mature at the smallest sizes, bear the largest eggs, and produce the greatest numbers of eggs at the smallest maternal body sizes.

TABLE 38. Geographical variation in the linear regressions relating egg size (diameter in mm) to maternal length (mm) in brook trout.

Location	Slope	Intercept	Range in maternal length (mm)	Reference
Dunk R., P.E.I.	0.0082	1.89	164-393	Johnston & McKenna (1974)
Laurentide, Québec	0.0007	4.05	155-450	Vladykov (1956)
Tomtit Run, Pennsylvania	0.0090	2.71	117-211	Wydoski & Cooper (1966)
L. Laflamme, Qué.	0.0031	3.22	189-282	Verreault & Langlois (1984)
Freshwater, Newfoundland	0.0120	3.20	72-148	present study
Cape Race R., Nfld.	0.0210	1.83	96-137	"
Cripple Cove, Nfld.	0.0060	2.96	119-197	"
Watern Cove, Nfld.	0.0180	1.88	97-165	"
Drook R., Nfld.	0.0140	2.10	108-175	"
Wrights R., Nfld.	0.0100	2.82	101-138	"
Whalens R., Nfld.	0.0110	2.69	94-144	"

4.1.2 The Influence of Growth and Egg Size on Large-Scale Patterns of Variation

Variation in growth is not associated with variation in latitude. There is no correlation between latitude and growth throughout the geographical range of the brook trout (all data: $r=0.01$, $p=0.53$, $n=35$; Sept. and Oct. data only: $r=0.20$, $p=0.35$, $n=20$). This reflects the large variation in growth on a small scale within latitudes (cf. Table 36). For example, length at the end of the third year ranged from 132 to 243 mm at 41° N latitude in Pennsylvania, from 93 to 203 mm at 46° N, and from 112 to 295 mm at latitudes greater than 50° N.

Large-scale variation in egg size is negatively associated with variation in growth (Fig. 19). There is a significant negative correlation between egg size and third year length among the ten populations for which data are available ($r=-0.83$; $p<0.01$). If slower growth is indicative of lower food supply to juveniles and adults, then the negative correlation between egg size and growth supports the prediction that reduced food abundance favours the production of large eggs (see section 4.2.3).

Large-scale variation in the slopes of the fecundity-maternal length regressions is associated with variation in egg size (Fig. 20). Egg size was standardized to a maternal

FIGURE 19. Egg size plotted against growth for ten populations of brook trout (population codes: CC=Cripple Cove, CR=Cape Race, D=Dunk, DR=Drook, FW=Freshwater, LF=Laflamme, T=Tomtit WC=Watern Cove, WH=Whalens, WR=Wrights).

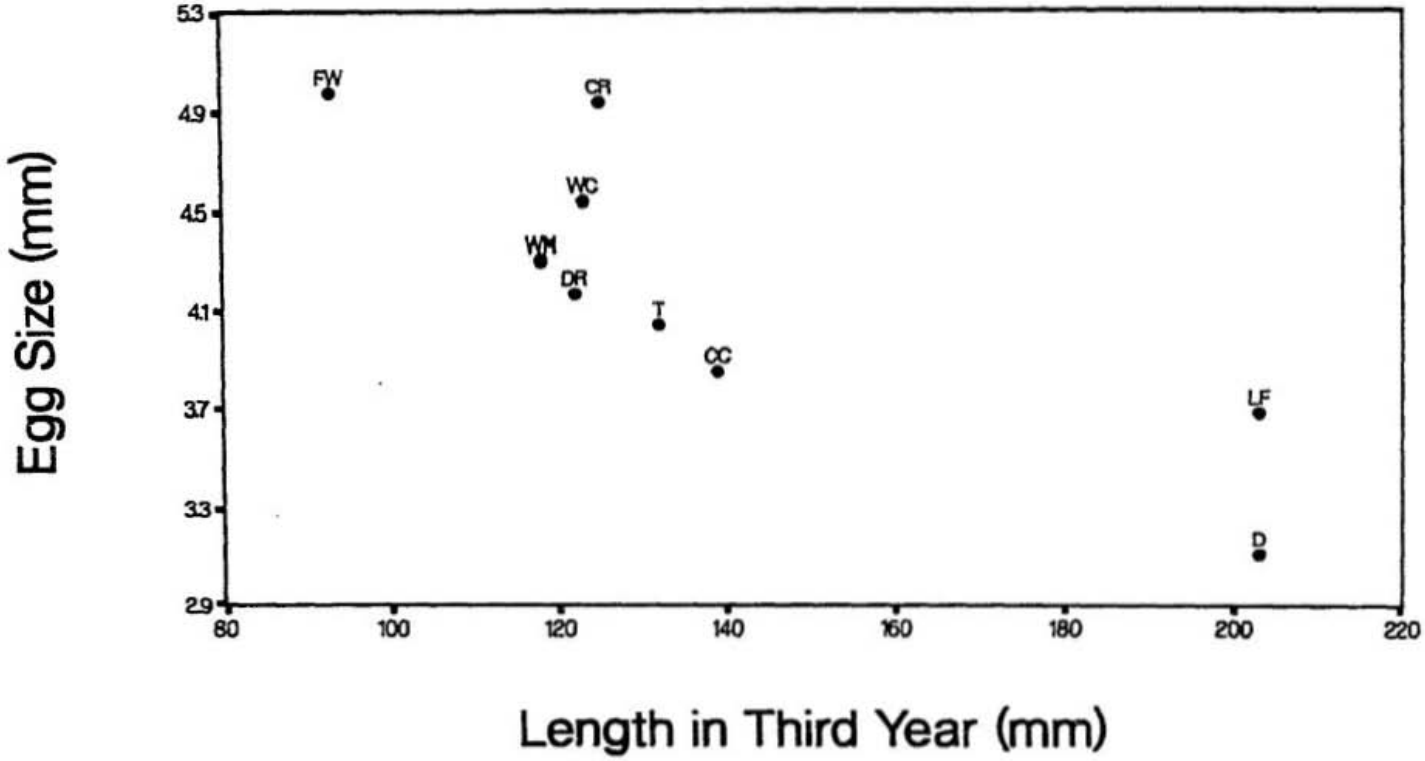
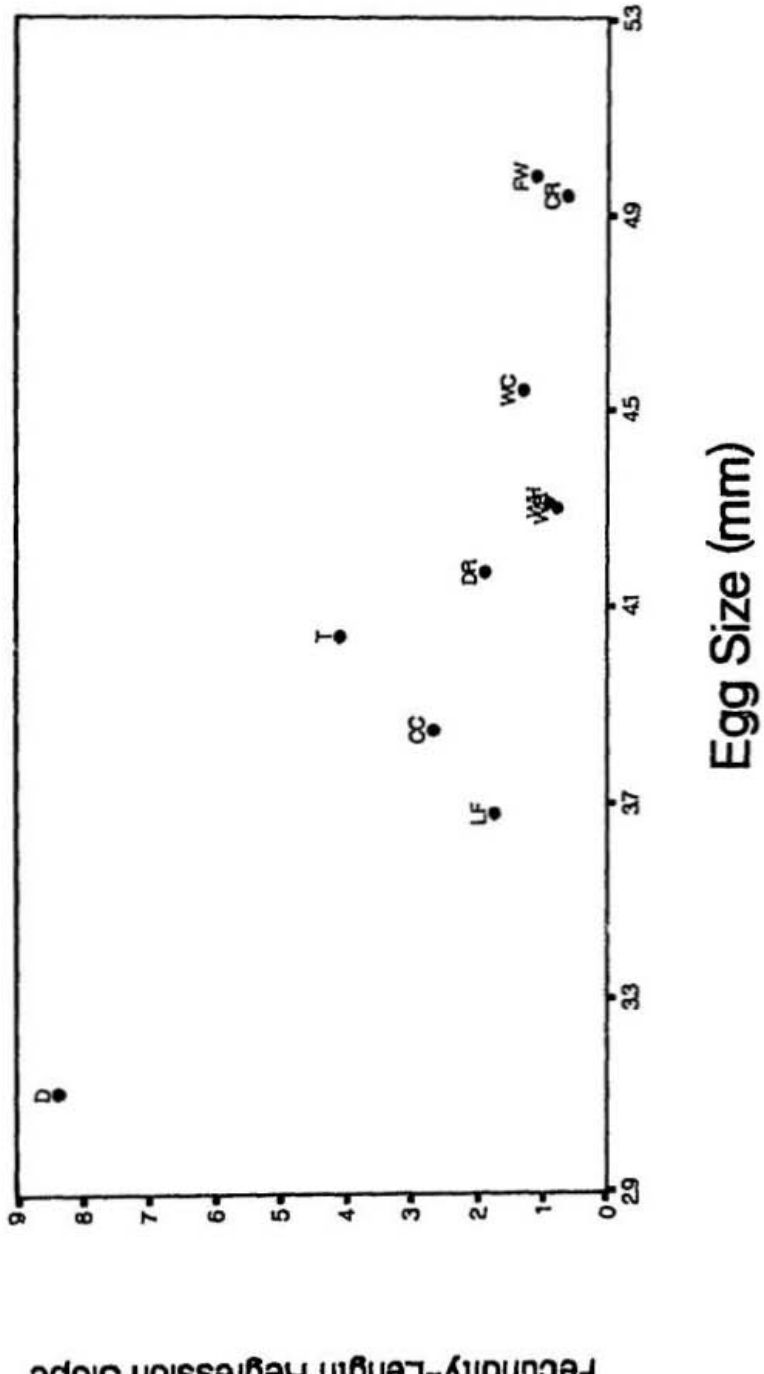

Egg Size (mm)
53
49
45
41
37
33
29
FW
CR
WC
WM
DR
T
CC
LF
D
80
100
120
140
160
180
200
220
Length in Third Year (mm)

FIGURE 20. Relationship between the fecundity-length regression slopes and egg size among ten populations of brook trout (population codes as in Fig. 19).


Fecundity-Length Regression Slope
Egg Size (mm)
0
1
2
3
4
5
6
7
8
9
29
33
37
41
45
49
53
D
LF
OC
T
DR
WC
FW
OR

length of 148 mm (the mid-range size at maturity for the 10 populations in Table 37) to incorporate maternal length effects on egg size. Among populations, the fecundity-maternal length slope is negatively correlated with egg size ($r=-0.76$; $p<0.01$). This is to be expected if the proportion of the body available for gonadal production is roughly constant among populations. That is, as egg size increases, the rate at which eggs can be produced per unit body length must decrease.

4.1.3 Clinal Patterns of Life History Variation

The utility of using large-scale variation to explain biological patterns and processes depends on the nature of the variation that requires explanation. For some problems in biology, clinal (e.g. latitudinal, altitudinal) variation can be used to confirm specific hypotheses. For example, the study of the ecological effects of spatial patterning on ecosystems (i.e., landscape ecology) requires comprehensive descriptions over broad spatial scales for hypothesis testing (Turner, 1989). This is because the processes effecting the observed variation occur at a large scale (e.g. ecosystems). However, the use of clinal descriptions in studies of variation effected by small-scale (e.g. population) processes should be restricted to exploratory

analyses and to hypothesis formulation rather than hypothesis testing.

The present study illustrates how variable life histories can be among reproductively discrete populations inhabiting a very small geographical area. Thus, depending upon the problem of interest, conclusions drawn concerning variation among populations at different points along a gradient may be valid only when contrasted with variation among populations at a single location.

4.2 The Evolution of Egg Size and Egg Number

4.2.1 The Trade-Off Between Egg Size and Egg Number

The evolution of egg size and egg number ultimately depends on the relationship between egg size and offspring fitness and on the influence this relationship has on parental fitness (Svärdson, 1949; Lack, 1954; Smith and Fretwell, 1974; Morris, 1987). If offspring fitness is independent of offspring size, then the evolutionarily stable strategy (ESS; sensu Maynard Smith, 1972) of investment per offspring should be to maximize the number of offspring, each approaching the physiologically minimum size, within a brood (Brockelman, 1975). However, if offspring fitness increases with offspring size, then the ESS of investment per offspring is attained when the

proportional gain in offspring fitness from an increment in parental investment equals the proportional parental loss in offspring numbers (Lloyd, 1987). This assumes that there is a trade-off between the size and the number of offspring that a female can produce. That is, if the energy available for reproduction at any given time is limited to a finite amount, energy expended to increasing offspring size is done so at the expense of producing fewer offspring (Smith and Fretwell, 1974).

There is strong empirical evidence of a trade-off between egg size and egg number in brook trout. Significant partial correlation coefficients between egg size and egg number (controlling for gonad weight) were negative for each of the Cape Race populations. For example, in a gonad weighing 4 grams (which corresponds to maternal lengths of 118, 131, 131, and 149 mm for Freshwater, Watern Cove, Cape Race, and Cripple Cove populations, respectively), an increase in egg diameter from 4 to 5 mm will result in a 24% (Freshwater) to 78% (Cripple Cove) decrease in egg number. Furthermore, the average rate of increase in reproductive biomass (egg number X egg volume) with gonad weight is the same among populations. Thus, the trade-off is qualitatively similar among populations. Differences in the intercepts of the regressions between reproductive biomass and gonad weight are indicative of proportionately different amounts of non-reproductive tissue in the gonads (e.g.

connective tissue). The population having the largest mature females (Cripple Cove) had the lowest intercept by a large margin (cf. Table 20). This may be indicative of a general relation between tissue biomass and the amount of supportive and maintenance tissue required to maintain that biomass.

In brook trout, the production of fewer eggs may be the primary evolutionary cost to the production of larger eggs. The maternal fitness model suggests that within broods, the trade-off between egg size and egg number is sufficient to negate the survival benefits of large eggs under abundant food conditions. Sargent et al. (1987) argued that increased mortality during the egg stage, through increased instantaneous egg mortality or increased developmental time, represents an evolutionary cost to large eggs. In the present study, embryonic survival and developmental time to hatching were independent of egg size (cf. Table 29). This independence of egg mortality and egg size may be due to non-limiting supplies of oxygen in the incubation chambers. In substrates where oxygen is limited, large coho salmon (Oncorhynchus kisutch) eggs suffer higher mortality than small eggs (van den Berghe and Gross, 1989). However, if females select the substrate and, indirectly, select the oxygen regime into which they bury their eggs, then oxygen limitation may not represent an important cost to the production of large eggs. If developmental time increases

with increasing egg size, it may be during the yolk resorption stage (Rombough, 1985). However, this may be compensated by the increased mobility of larger juveniles that results in feeding prior to complete yolk sac resorption (personal observation, this study). Although not denying the potential importance of developmental delays associated with large eggs, their effect on fitness may be minimal relative to the survival benefits accrued at the juvenile stage.

4.2.2 The Influence of Egg Size on Juvenile Survival

The results further document the survival advantages of large offspring size in early life observed in many animals (e.g. fish [Bagenal, 1969; Marsh, 1986; Henrich, 1988]; amphibians [Berger and Uzzell, 1977]) and some plants (Black, 1958; Schaal, 1980). The proximate advantages of large body size in early life for brook trout are probably related to behaviour. Intraspecific interactions among juvenile salmonids are governed by size-dependent, behaviourally-mediated dominance hierarchies (Brown, 1957). Grant (1990) found aggressive brook trout to be 13% larger than nonaggressive conspecifics in three southwestern Ontario streams. Abbott et al. (1985) reported that a weight advantage of 5% was sufficient to ensure dominance among juvenile rainbow trout, Oncorhynchus mykiss. Large,

dominant individuals intimidate, chase, and attack smaller subordinates. This limits a subordinate's food consumption, reducing both its growth rate (Koebele, 1985) and its fitness (Parker et al., 1989).

The smallest individuals experienced the highest mortality within broods in the present study. Furthermore, juveniles from large eggs had higher survival when competing with other large individuals than did juveniles from small eggs who competed with other small juveniles. Because greater energy reserves in larger individuals can reduce susceptibility to starvation (Bagenal, 1969; Marsh, 1986), subordinates within groups of large juveniles are probably better able to withstand the physiological stress imposed on them by intraspecific competition than are subordinates within groups of small individuals.

The empirically-based fitness functions derived here depend upon linear associations between offspring survival and offspring size (cf. Fig. 17). However, theoretical formulations generally assume that the function relating offspring size and survival within a population or a species is either concave downward (Smith and Fretwell, 1974; Winkler and Wallin, 1987) or logistic (Sargent et al., 1987; Lloyd, 1987). These functions include asymptotic values for which survival changes relatively little with changes in offspring size. But it may not be reasonable to expect such asymptotic offspring sizes to exist under natural

conditions. Under stabilizing selection, only a limited range of offspring size is expected, e.g. near the inflexion point of a logistic function. This would result in an approximately linear relation between offspring survival and offspring size when data are obtained from natural populations.

The influence of egg size on offspring survival, and thus maternal fitness, may have been underestimated here. The increased fitness accruing from the production of large eggs was based on competition among siblings of the same egg size. In natural populations, non-siblings from egg sizes varying by 1 mm or more in diameter compete for food and space (see Randall et al., 1986). This should accentuate the fitness differential between large and small juveniles (Parker and Begon, 1986; Parker et al., 1989).

4.2.3 Maternal Fitness Consequences of Variation in Egg Size and Food Abundance

Empirically-based model simulations in this study support the hypothesis that natural selection favours an increase in offspring size with reductions in resource abundance (Smith and Fretwell, 1974; Sibly and Calow, 1983; Kaplan and Cooper, 1984). In brook trout, decreasing availability of juvenile food selects for the production of smaller numbers of larger eggs. Large juveniles hatch from

large eggs and large juveniles have higher survival in early life than do small juveniles.

Field data from Cape Race support the hypothesis that population variation in egg size can be explained by differences in food abundance. (Implicit is the assumption that the invertebrate biomass estimates presented here are representative of long-term variation in food supply among streams.) The model simulations suggest that optimal egg sizes can differ by 0.9 mm between environments differing in juvenile food abundance by a factor of 2. Thus, the 3-fold difference in aquatic invertebrate biomass among the Cape Race streams would be sufficient for the development of different egg size optima. Furthermore, the populations producing the largest eggs inhabited the streams having the lowest invertebrate biomass (Freshwater and Cape Race).

The non-additive effects of food abundance and egg size on juvenile survival, coupled with the maternal trade-off between egg size and egg number, results in different optimal egg sizes for environments differing in the abundance of juvenile food. Environmental interactions on the relation between offspring size and survival traits are necessary for the development of environment-specific offspring size optima. At large egg sizes, reductions in food abundance have little effect on juvenile brook trout survival. In contrast, at small egg sizes, reductions in food abundance significantly reduce the probability of

juvenile survival. Empirical evidence of such interactions is available for amphibians. Kaplan (1985) reported non-additive effects of egg size and food abundance on time to metamorphosis in the California newt, Taricha torosa. A significant developmental time X ovum size interaction on offspring has recently been found in the Oriental fire-bellied toad, Bombina orientalis (R.H. Kaplan, unpubl.). Food abundance significantly influences size at metamorphosis in the tree frog, Rana sylvatica, (Berven and Chadra, 1988) and in the California newt (Kaplan, 1985) although these effects are not influenced by egg size.

4.2.4 Reproductive Strategies in Temporally Variable Environments

The data presented here indicate that when the environment changes little from year to year, selection should favour the production of a single egg size within a brood. However, the generality of the conclusion that selection optimizes egg size in natural populations has been questioned (e.g. Sargent et al., 1987) because of the considerable variation in offspring size in many organisms. Such intrapopulational variability is common within species of salamanders (Kaplan, 1980), frogs (Crump, 1981), fish (Marsh, 1986) and plants (Michaels et al., 1988). Within-brood variation in offspring size has been explained as an

adaptation to a variable environment (Capinera, 1979). Kaplan and Cooper (1984) predicted that variable environments should select for variable offspring sizes. For example, they argued that the differences in developmental and growth rates generated by variable egg sizes allow tropical tree frogs reproducing in temporary ponds to produce at least a few eggs having the appropriate size for the conditions that prevail.

The fitness functions derived here provide an empirical basis for testing the hypothesis that selection should favour the production of variable sized offspring in an unpredictable, temporally-varying environment. (Variability is a relative term discussed here as an intra-generational phenomenon). Organisms can achieve this by varying offspring size within or among broods. I consider both strategies here.

I assumed that the environment varies randomly from high to low levels of juvenile food abundance on an annual basis and that females produced a biologically reasonable maximum number of five broods in a lifetime. When modelling the fitness consequences of varying egg size among broods, I assumed that egg size was constant within broods and that egg size equalled randomly one of two possible sizes among broods.

Using females from the Watern Cove population, I evaluated the fitness consequences of adopting each of the

following strategies. The fitness consequences of within-brood variability in egg size was examined in strategies I-VI whereas the consequences of randomly varying egg size among broods was examined in strategies VII-IX.

Strategy	Constancy of Egg Size Within Broods	Among Broods	Egg Size (mm)
I	constant	constant	3.90 ± 0.00
II	constant	constant	4.70 ± 0.00
III	constant	constant	4.30 ± 0.00
IV	variable	constant	4.30 ± 0.10
V	variable	constant	4.30 ± 0.20
VI	variable	constant	4.30 ± 0.30
VII	constant	variable	3.90 or 4.70
VIII	constant	variable	3.90 or 4.30
IX	constant	variable	4.30 or 4.70

The egg sizes for strategies I and II are the optimal egg sizes for Watern Cove females in high and low food environments, respectively. The egg size of 4.30 mm is midway between the optima and I considered three levels of variability associated with this egg size. Females adopting strategies IV, V, and VI produced three egg sizes within a brood (the mean egg size and the egg sizes corresponding to the mean plus and minus 1 s.d.). Temporal environmental heterogeneity was simulated first by assigning a unique number for each of the environments (1=high food supply; 2=low food supply; see Appendix A) and then by randomly sampling 5 numbers from a distribution of ones and twos (n=100; 1:1 ratio). The fitness of each strategy was evaluated for each of 20 randomizations with the running

mean fitness (i.e., total number of surviving juveniles produced in a lifetime) shown in Figs. 21 and 22.

The simulations do not support the hypothesis that egg size variation has evolved as an optimal solution to unpredictable environments. For brook trout and the fitness functions considered here, unpredictable temporal variability selects for constancy in egg size both within and among broods. The optimal egg size was intermediate to those optimizing fitness at the environmental extremes (i.e., high and low food).

The results agree with McGinley et al.'s (1987) theoretical modelling which indicated that selection generally favours equal investment among offspring within broods in temporally heterogeneous environments. The simulations also suggest that environmental constancy is not a prerequisite for the existence of optimal egg sizes. Selection may favour an optimal egg size if the environment varies randomly between predictable extremes.

The reduced fitness associated with offspring size variation may have been a function of the form of environmental variation considered here. If the environment was allowed to vary randomly among n different environmental states rather than just two extremes, then investment into variable offspring size either within or among broods may be represent an adaptive alternative. Empirical evaluation of

FIGURE 21. Maternal fitness consequences of producing offspring of variable and constant sizes within broods in temporally heterogeneous environments (data are running mean fitnesses).

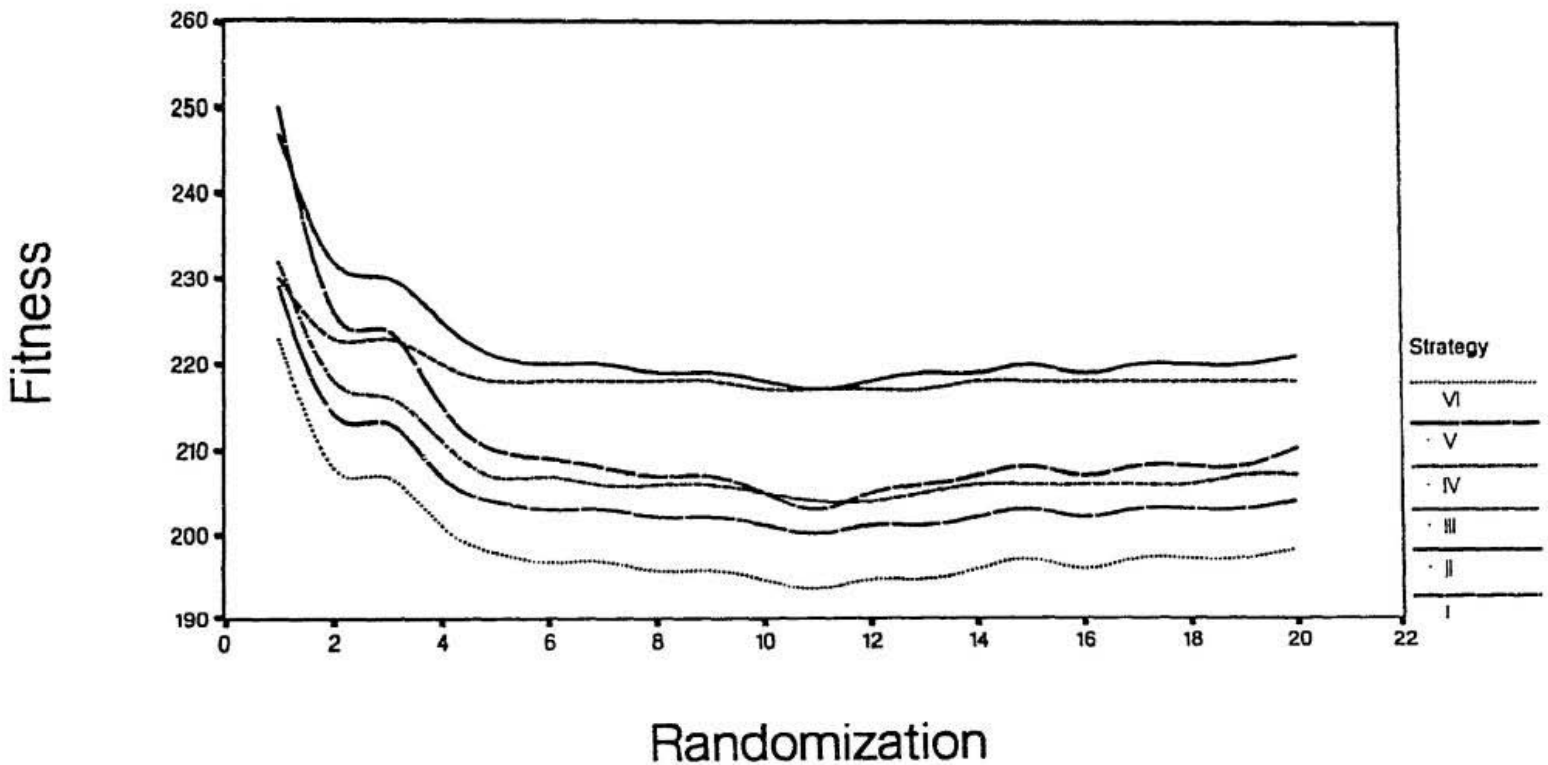
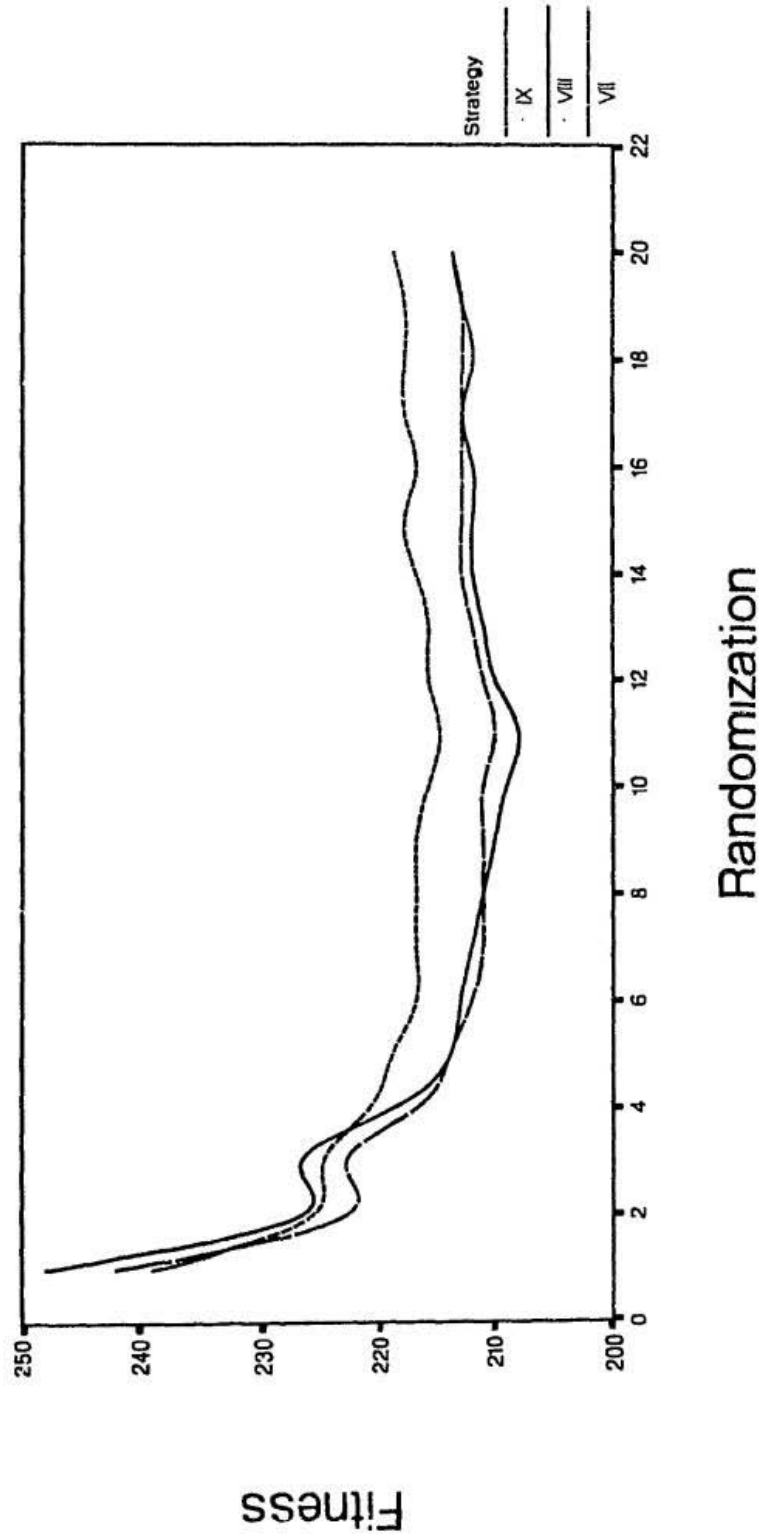

Fitness
260
250
240
230
220
210
200
190
0
2
4
6
8
10
12
14
16
18
20
22
Randomization
Strategy
VI
V
IV
III
II
I

FIGURE 22. Maternal fitness consequences of producing offspring of variable and constant sizes among broods in temporally heterogeneous environments (data are running mean fitnesses).


Fitness
250
240
230
220
210
200
0
2
4
6
8
10
12
14
16
18
20
22
Randomization
Strategy
IX
VIII
VII

this prediction would require knowledge of offspring survival probabilities in each environment and the probabilities that any given environmental condition will exist at any one time.

4.3 The Interrelation Between Age and Size at Maturity and Size-Specific Fecundity

4.3.1 Age-Specific Survival Probabilities in Brook Trout

The age-specific survival estimates used here (cf. section 3.10) conform to a set of probabilities that are reasonable for each population. Assuming that each population is neither increasing nor decreasing in number, populations are constrained in such a way that they reproduce themselves every generation. In a sexually reproducing population, each female must produce two offspring (1 male and 1 female, assuming a 1:1 sex ratio) that survive to reproduce. Therefore,

$$(\bar{m})\ (l_e)\ (l_{sf}l_{wf})\ \left(\sum_{f}^{\alpha} l_{sx}l_{wx}\right)^{\alpha-2}\ (l_s) = 2 \qquad (15)$$

where $\bar{m}$ is the mean population fecundity (cf. Table 6), l_e is the survival from fertilization to exogenous feeding as fry, $l_{sf}l_{wf}$ is the survival rate from exogenous feeding to

age f=1.67, l_{sx} and l_{wx} are summer and winter survival rates for non-fry (cf. Table 32), respectively, and α equals the modal age at first reproduction (cf. Table 31).

The survival rates for eggs and fry derived from equation (15) are reasonable for brook trout populations. Substitution of the estimated values of l_s, l_w, and m into equation (15) yields ($l_e l_{sf} l_{wf}$) values (for which I do not have empirical data) of 0.16, 0.13 and 0.06 for Freshwater, Cripple Cove and Watern Cove, respectively. Choosing a realistic value of 0.69 for l_e (average of 0.59 [Hausle and Coble, 1976] and 0.79 [Brasch, 1949]) yields annual fry survival rates of 0.23 (Freshwater), 0.19 (Cripple Cove) and 0.09 (Watern Cove). These values are 32-90% less than the estimated annual survival rates for non-fry and concur with Power's (1980) observation that high mortality during the first few months of life are found by virtually all studies of brook trout population dynamics. Fry survival rates for other salmonids range from estimates of 0.10 and 0.13 for two populations of brown trout, Salmo trutta (Elliott, 1989) to 0.33 for Atlantic salmon (Hutchings and Myers, 1986). And substituting the winter survival rates of immature non-fry for l_{wf} (cf. Table 29) and 0.69 for l_e produces survival rates from fertilization to the end of the first summer that range from 0.14 to 0.40. These are within the range of 0.036 to 0.424 for brook trout reported by Smith (1944).

The survival rates calculated for non-fry are not unreasonable estimates for brook trout. Annual survival rates for immature Cape Race trout were estimated to be 0.34 (Freshwater), 0.43 (Cripple Cove) and 0.55 (Watern Cove). These estimates are similar to those of equivalent ages reported by Wiseman (1969) in other minimally exploited Newfoundland populations (mean survival rates: 0.47 - Indian River; 0.49 - Berry Hill Pond; 0.36 - Big Bear Cave Pond; 0.35 - Indian Bay Big Pond). Finally, the estimated summer survival probabilities for the Cape Race trout (0.81, 0.85 and 0.89 as calculated from the static life tables) are similar to those reported by Elliott (1989) for two populations of brown trout in England (0.823 and 0.897).

4.3.2 Evidence of Adaptive Variation in Age at Maturity

Optimal age at maturity represents a balance between the benefits and the costs associated with investing energy into present versus future reproduction. The benefits of maturing early in life are that an individual maximizes both its rate of gene input into the population and its probability of surviving to reproduce. The costs include reduced fecundity and decreased probability of surviving to reproduce in the future. Selection for age at maturity also depends on population dynamics (Charlesworth, 1980). In an increasing population, mutations that decrease age at

maturity will generally be favoured whereas mutations that delay reproduction will be favoured when populations are decreasing in size.

The similarity of the predicted and observed ages at first reproduction (cf. Tables 33, 35) provides preliminary evidence that population variation in age at maturation is adaptive. The predicted age at first reproduction for Freshwater (2 yr) equals the observed age at first reproduction observed in the field although most females did not mature until age 3. The modal female age at maturity (3 yr) in Watern Cove equals the predicted age at first reproduction. With one exception, the observed age at first reproduction in Cripple Cove equals the predicted age although most females did not mature until age 4. (The single Cripple Cove female which matured at age=2 attained a length of 119 mm, a size and a consequent fecundity high enough to make her age at maturity evolutionarily stable [r^{*}=1.83; cf. Table 33]). The modal ages at maturity in Cripple Cove (4 and 5 yrs) are slightly higher than the predicted ages at first reproduction of 3 and 4 yrs. The implicit assumption that age at maturity is maintained by stabilizing selection is supported by the similarity between observed and predicted optimal ages at maturity in 23 teleost species as reported by Roff (1984).

Within-population variation in age at maturity and a lack of complete correspondence between predicted and

observed reproductive ages is not surprising. Maynard Smith (1972) and Schaffer and Rosenzweig (1977) have provided the theoretical underpinnings for the existence of alternative age- and size-specific reproductive strategies within populations. Empirical evidence of alternative male reproductive strategies in fish exists for male Atlantic salmon (Jones, 1959; Hutchings and Myers, 1988), bluegill sunfish, Lepomis macrochirus, (Gross and Charnov, 1980), and coho salmon, Oncorhynchus kisutch, (Gross, 1985). Using life history theory to predict norms of reaction for age and size at maturation, Stearns and Koella (1986) concluded that most organisms mature neither at a fixed size nor age but at some point along an age-size trajectory. The location of the point depends on the relationship between changes in growth rate and changes in adult and juvenile mortality.

The lack of complete correspondence between predicted ages at first reproduction and modal ages at maturity can be attributed to the restrictive assumptions of the analysis. For example, selective disadvantages associated with maturation at a small size are excluded from the analysis. The Euler-Lotka equation does not account for either age- or size-dependent variability in breeding success (e.g. mate acquisition, territory establishment and defence, depth at which eggs are deposited - all of which are strongly correlated with body size [van den Berghe and Gross, 1989]). The equation also assumes that all eggs have the same

probability of survival (i.e., there is no variation in egg size). Despite these limitations, the close agreement between the predicted and the observed ages at maturity among the 3 populations supports the hypothesis that the observed ages at maturation are evolutionarily stable and are, therefore, adaptive.

4.3.3 Adaptive Variation in Relative Fecundity

Evidence of adaptive variation in size-specific fecundity is based on the observation that the substitution of size-fecundity regressions among populations results in sub-optimal fitnesses within populations (Table 39).

There is selection for early reproduction in Freshwater and Watern Cove populations relative to Cripple Cove. The older optimal age at first reproduction for Cripple Cove females is due primarily to the low size-specific fecundities of age=2 females relative to those in Freshwater and Watern Cove populations. If the size-fecundity regression for Freshwater females is substituted for that of Cripple Cove females, fitness is maximized when Cripple Cove females initially reproduce at age=2 (r^{*}=1.30 and 1.06 for females of age 2 and 3, respectively).

Table 39. Modified intrinsic rates of increase (r^*) for different ages at first reproduction (α) for Freshwater and Watern Cove populations using the length-fecundity regressions for the populations indicated in parentheses (FW=Freshwater; WC=Watern Cove; CC=Cripple Cove).

Population	α	r^*(FW)	r^*(WC)	r^*(CC)
Freshwater	2	1.10	-0.10	-0.36
	3	0.77	0.58	-0.03
	4	0.40	0.33	-0.11
	5	0.12	0.09	-0.03
Watern Cove	2	-	0.54	0.03
	3	-	1.05	0.55
	4	-	0.83	0.80
	5	-	0.64	0.67

4.3.4 The Influence of Growth on Age and Size at Maturity

The influence of growth rate on the covariation in age and size at maturation is strongest among, but not limited to, organisms whose growth is approximately indeterminant (i.e., individuals increase in body size continually, albeit at a gradually decreasing rate, throughout their life). Five patterns are reported in the literature (Myers, 1982; Stearns and Koella, 1986). Relative to faster growing individuals, slower growing individuals (1) mature later in life at a smaller size (e.g., brown trout, Salmo trutta, [Alm, 1959]; the copepod Eurytemora herdmani [McLaren, 1974]; male slider turtles, Pseudomys scripta, [Gibbons et al., 1981]) (2) mature later at the same size (e.g. American plaice, Hippoglossoides platessoides, [Pitt, 1975]), (3) mature later in life at a larger size (e.g. Drosophila melanogaster [Robertson, 1963]; Gammarus lawrencianus [Doyle and Myers, 1982]), (4) mature earlier at a smaller size (e.g. Arctic char [Jonsson and Hindar, 1982; Svedäng, 1990]), or (5) mature at the same age at a smaller size (female slider turtles [Gibbons et al., 1981]).

Myers (1982) argued that the influence of growth on age and size at maturity should be analysed among individuals within populations. Available data on size and age at maturity from the Cape Race populations are consistent with the first pattern indicated above (i.e., increased growth

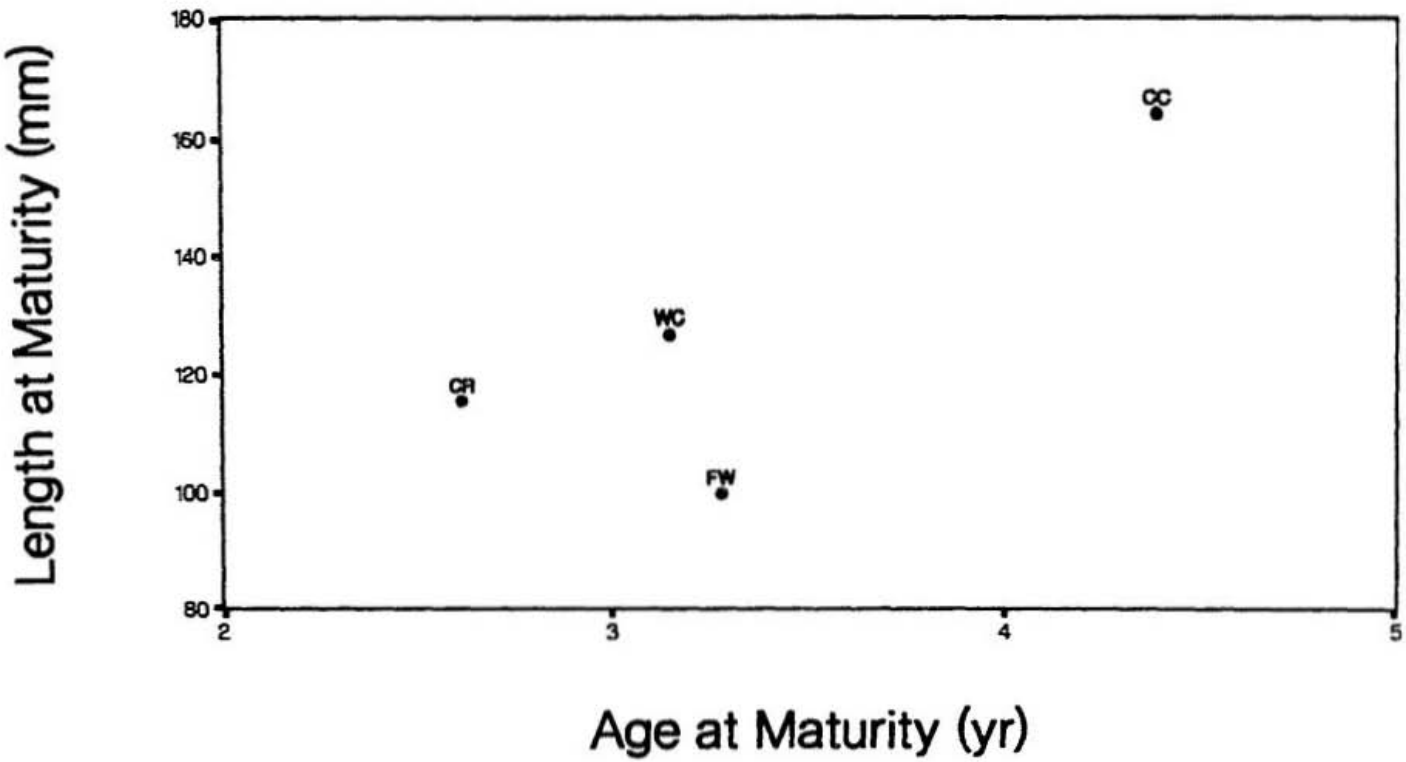
rate leads to earlier maturation). In Freshwater (n=18), Cape Race (n=20), Cripple Cove (n=1), and Watern Cove (n=15) populations, the average length of the youngest mature females was longer than the average estimated length of immature fish of the same age (Table 40). In Watern Cove and Cripple Cove, the average length of the youngest mature females during spawning exceeded the lengths of immature fish of the same cohort in the following June.

The relationship among growth, age at maturity and size at maturity in Freshwater, Watern Cove and Cape Race populations also conforms with that of the first pattern indicated above. That is, individuals in the population having the slowest individual growth rate (Freshwater) mature at the oldest age and at the smallest size relative to individuals in the other two populations (Fig. 23). However, relative to these 3 populations, Cripple Cove females mature significantly later in life and larger in size despite having a relatively fast growth rate. A comparison of the most divergent populations yields the fourth pattern of covariation indicated above. Relative to Cripple Cove females, slower growing Freshwater females mature earlier at a smaller size.

Table 40. Lengths (mm) of mature female brook trout at age=2, estimated lengths (mm) at age=2 for immature trout, and actual lengths (mm) of immature trout at age=2.67 (i.e., June).

	Mature	Immature	
Population	Age=2	Age=2	Age=2.67
Freshwater	81.1	73.4	83.4
Cape Race	106.3	78.0	116.3
Cripple Cove	119.0	77.1	112.4
Watern Cove	109.8	75.3	107.2

FIGURE 23. Scatterplot between mean age and mean body size at maturity for female brook trout in four Cape Race populations (population codes as in Fig. 19).


Length at Maturity (mm)
180
160
140
120
100
80
2
3
4
5
CC
WC
GI
FW
Age at Maturity (yr)

4.4 Population Variation in Reproductive Effort

4.4.1 Gonadosomatic Index as a Measure of Reproductive Effort

I have assessed reproductive effort in brook trout by directly measuring gonadal mass as a proportion of total body weight (the gonadosomatic index or GSI). Williams (1966) considered this proportion to be a reasonable approximation of reproductive effort.

Probably the most important disadvantage associated with using the GSI as a measure of reproductive effort in salmonids is that it excludes potential costs associated with the behavioural components of reproduction (e.g. territory defence, mate acquisition, nest construction). (In comparison with the oceanic migrations of Pacific and Atlantic salmon, physiological costs associated with migration to the spawning substrate are probably negligible on Cape Race, given the low discharge of the streams and the minimal potential migration distances of 0-2 km.) It seems reasonable, however, to expect behavioural costs to be inversely related to body size. Breeding success is positively correlated with body size in male and female coho salmon (van den Berghe and Gross, 1989). The probability of mortality resulting from mate competition appears to increase with decreasing body size in male Atlantic salmon

parr (Hutchings and Myers, 1987) and in male brown trout (Bohlin, 1977). And, for a given size of substrate particles, smaller females may incur greater physical damage to their caudal peduncle during nest construction than larger females. (Autumn collections in Freshwater and Watern Cove rivers indicate that choice of spawning substrate was independent of body size.) This posited cost to small females may be negated if larger brook trout females dig deeper nests (cf. van den Berghe and Gross, 1984).

Despite its exclusion of some potential physiological costs, the GSI probably represents a reasonable first approximation of reproductive effort in brook trout. Hereafter, GSI will be used as though synonymous with reproductive effort.

4.4.2 Population Variation in Reproductive Effort

GSI varied among individuals within populations and among populations from the small geographical area of Cape Race.

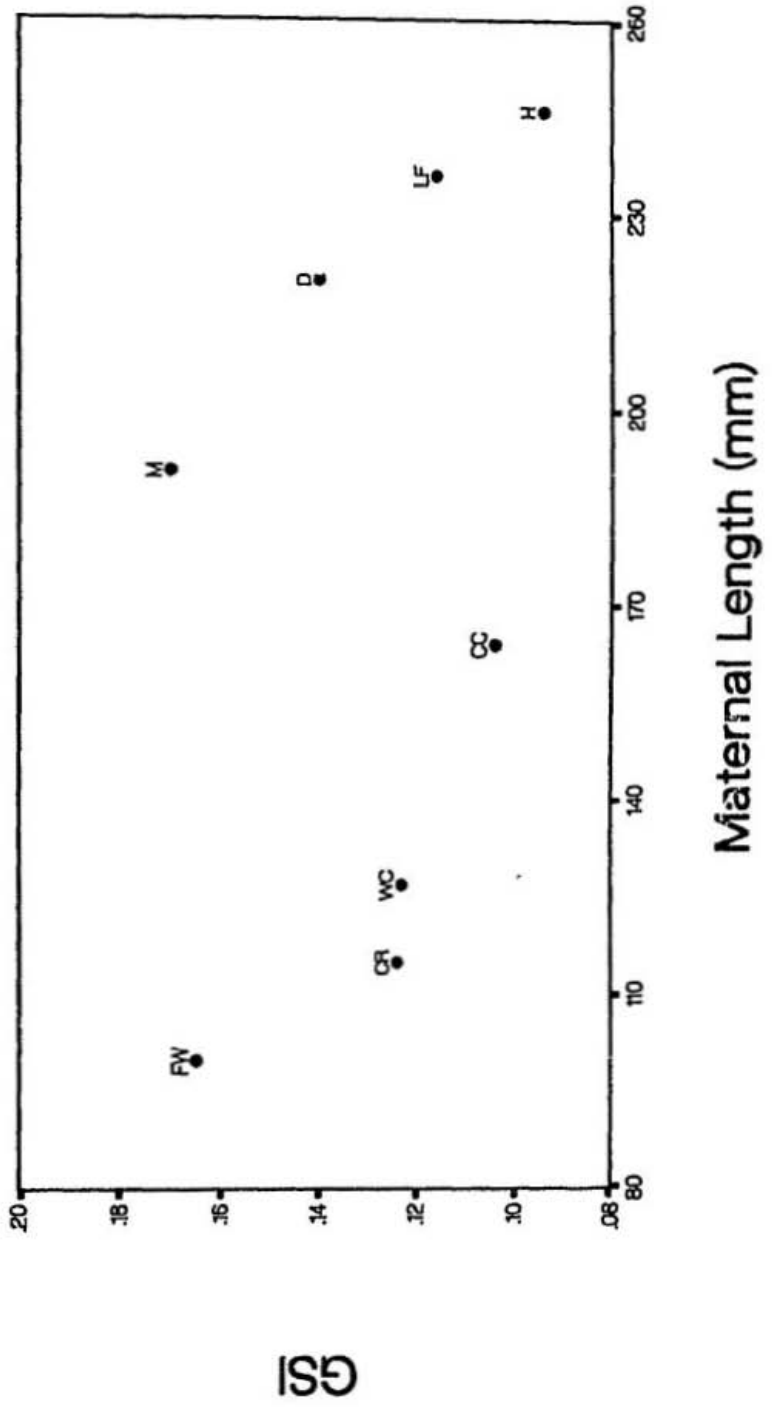
Within three populations, the GSI was significantly, albeit weakly, associated with variation in body size. Although comparable data are few, there is a tendency for GSI to increase with body size within the Dunk River population, P.E.I., (Johnston and McKenna, 1974) but not for

females in Lac Laflamme, Québec, (Verreault and Langlois, 1984).

Body size does not account for variation in GSI among populations (Fig. 24). Ranging from 0.10 (Cripple Cove) to 0.16 (Freshwater), the proportional allocation of body tissue to gonads varied by 60% among the Cape Race populations. The range in individual GSI within the Cape Race populations (0.06-0.26) encompasses most of the range that has been documented for this species. Mean GSI for several Québec populations varies from 0.09 (Lac Hamon, an acidic lake; Moreau et al., 1982) and 0.12 (Lac Laflamme; calculated from data in Appendix 4 in Verreault and Langlois, 1984) to 0.14 (Laurentide lakes; Vladykov, 1956) and 0.17 (Lac Mignon, an alkaline lake; Moreau et al., 1982). In Pennsylvania populations, 10% of the total weight of mature fish was gonads (Wydoski and Cooper, 1966). Coleman (1970) reported that the GSI for female trout in the Koksoak River, Ungava Bay, was generally between 0.09 and 0.10, reaching a maximum of 0.15. Age-specific GSI ranged from 0.08 to 0.20 for females in the Dunk River, P.E.I. (Johnston and McKenna, 1974).

Population variation in GSI raises several questions. Why does such variability exist? Is population variation in GSI adaptive? Are there costs either to future survival or to future fecundity accruing from effort expended during

FIGURE 24. Scatterplot between GSI and maternal length among several brook trout populations (population codes as in Fig. 19 except M=Mignon and H=Hamon).


GSI
Maternal Length (mm)
.20
.18
.16
.14
.12
.10
.08
80
110
140
170
200
230
260
FW
CR
WC
CC
M
D
LF
H

present reproduction? If they exist, do costs of reproduction vary among populations?

4.4.3 Evidence of Adaptive Variation in Reproductive Effort

Population variation in GSI is the result of differences in both the size of eggs and the number of eggs produced by females of a given size. Among the Cape Race populations, for example, Freshwater females mature at the smallest size, produce the largest eggs (in absolute and in relative terms), have the highest size-specific fecundity to lengths of 140 mm, and have the highest proportional allocation of body tissue to gonads.

There is evidence that population variation in egg size and fecundity is adaptive. Based on laboratory manipulations and on model simulations presented here and elsewhere (e.g. Sibly and Calow, 1983), the production of large eggs should be favoured in environments characterized by low food abundance. The supposition that population variation in egg size represents a continuum of adaptive responses to variability in food resources is supported by field data. The biomass of stream invertebrates (the primary food source of brook trout [Power, 1980]) in Freshwater River - the population producing the largest eggs - is one-third the invertebrate biomass in Cripple Cove and Watern Cove rivers - the populations producing the smallest

eggs. The analyses of evolutionarily stable ages at maturity demonstrated that Freshwater females would be unable to replace themselves if they produced fewer eggs for their body size than was observed empirically. Similar conclusions can be drawn for the size-specific fecundities that have evolved in the Watern Cove population. However, despite the increase in size-specific fecundity in Freshwater females, individual fecundity remains low (average of 44 eggs per female). This low fecundity may act as an additional factor favouring the production of large eggs. Given their improbability of reproducing more than once, the low fecundity of Freshwater females may favour the production of large eggs by maximizing the probability that two offspring will survive to reproduce.

There is reason to believe, then, that among-population variation in reproductive effort is adaptive and that the observed population variation has a genetic basis. The best evidence against a non-adaptive explanation emerges from laboratory studies of the effect that increased food supply has on egg number. Under decreased food conditions, Scott (1962) reported that rainbow trout produced significantly fewer eggs per unit body mass although egg size remained unchanged. In the laboratory, I raised 67 trout from Freshwater, Cripple Cove, and Watern Cove populations from yolk sac resorption to maturity under high food conditions. In all populations, females grew significantly faster in the

lab than they did in the wild and they attained sexual maturity in less than 12 months (Appendix B). Size-specific fecundity increased under these high food conditions. This experimentally achieved phenotypic response to changes in food supply is opposite to that observed for the Cape Race populations. In the wild, size-specific fecundity generally increased as food supply decreased among populations. Thus, there is strong evidence that population variation in these reproductive variables is not wholly environmental in origin.

4.5 Costs of Reproduction

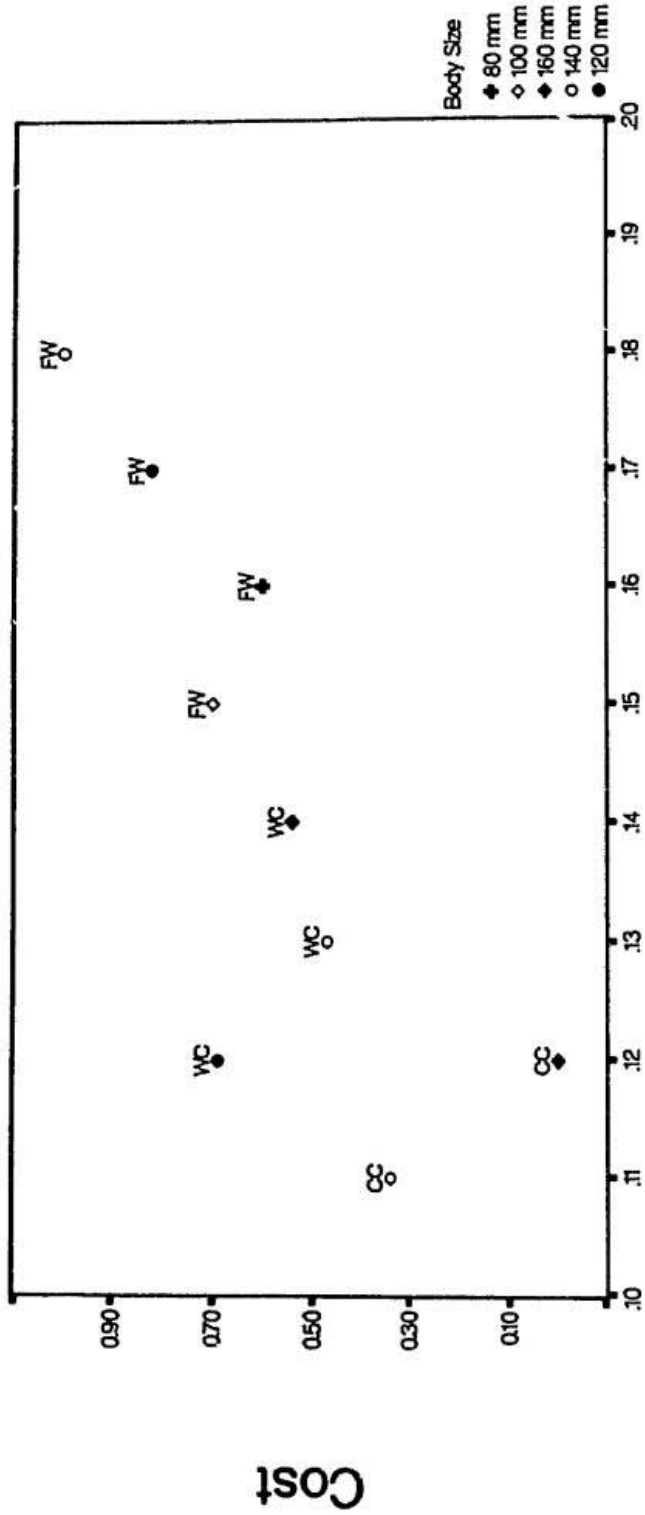
Variation in reproductive effort has resulted in differential costs of reproduction among the Cape Race populations. The high reproductive effort among Freshwater females is attained at a high cost to future survival and future reproduction. Alternatively, reproduction is less costly for Cripple Cove females whose reproductive effort is relatively small. The shapes of the cost functions provide an empirical basis for previous theoretical predictions and introduce the possibility that multiple cost functions can exist in a single population.

4.5.1 Reproductive Costs Among Populations

There is good reason to believe that brook trout experience a fecundity cost of reproduction. The reduction in growth rate with increasing age in the Cape Race populations is evidence of the growth reduction concomitant with maturation in fish (cf. Wootton and Evans, 1976; see references in Bell, 1980). Reductions in length resulting from maturation for current reproduction will reduce fecundity during later reproduction because of the physical constraints imposed by body size on the number of eggs a female can produce. This fecundity cost appears to be widespread among poikilotherms and represents a necessary condition for the existence of an optimal age at maturity (Bell, 1980).

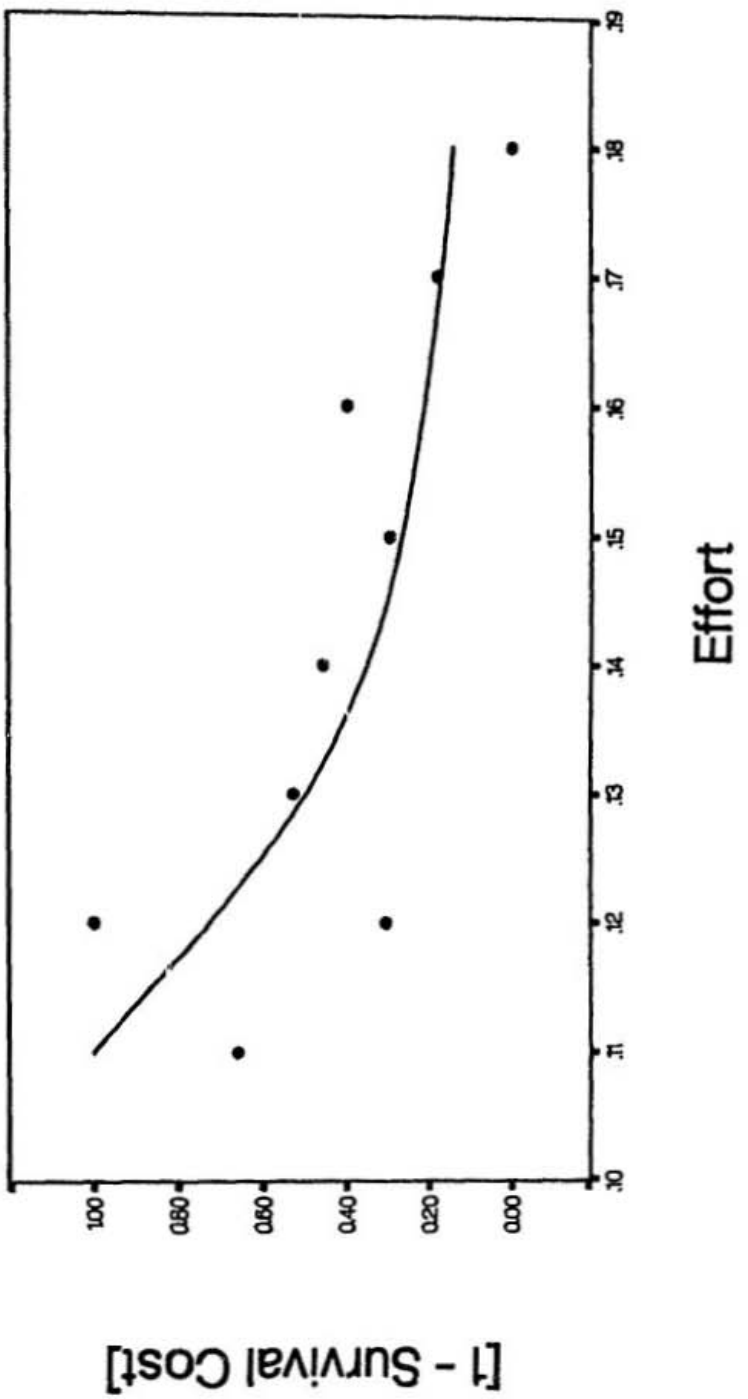
Empirical data from the Cape Race populations provide strong evidence of costs of present reproduction to future survival. Reproduction reduces the probability of overwinter survival by 31-62% within Freshwater, Cripple Cove and Watern Cove populations (cf. Table 29). Controlling for maternal size, costs increase with effort among populations in a convex upwards fashion (Fig. 25). (Survival costs are defined as the proportional reduction in overwinter survival probability for mature females relative to immature fish).

FIGURE 25. Size-specific costs of reproduction in three Cape Race brook trout populations (population codes as in Fig. 19).


Body Size
80 mm
100 mm
160 mm
140 mm
120 mm
FW
WC
CC
.10
.11
.12
.13
.14
.15
.16
.17
.18
.19
.20
.010
.030
.050
.070
.090
Cost
Effort

The effects of the shapes of cost functions have been considered theoretically by Gadgil and Bossert (1970), Schaffer (1974a,b), Schaffer and Rosenzweig (1977), and most recently by Bell (1980). Gadgil and Bossert (1970) plotted cost against effort in their cost functions, Schaffer (1974) and Schaffer and Rosenzweig (1977) used combinations of plots of growth, fecundity and post-breeding survival against effort, while Bell (1980) plotted post-reproductive survival against fecundity. To facilitate comparison, I reconstructed Fig. 25 by plotting (1-[survival cost of reproduction]) against effort (Fig. 26). These data conform to a concave upward cost function. Bell (1980) argued (1) that such a curve has a point of unstable equilibrium at which fitness is minimized at some combination of fecundity and survival and (2) that such a curve could lead to population divergence into iteroparous and semelparous life history strategies through disruptive selection. Schaffer and Rosenzweig (1977) also postulated that cost curves that are convex upward at high effort (see the concave-convex curves in their Fig. 5) can lead to inter-population variation in life histories. They proposed that a population could have either a set of alleles corresponding to various degrees of iteroparity or alleles producing semelparity at different ages (Schaffer and Rosenzweig, 1977:69).

FIGURE 26. Relationship between (1-[survival cost of reproduction]) and reproductive effort (GSI) among three Cape Race brook trout populations (curve fitted by eye).

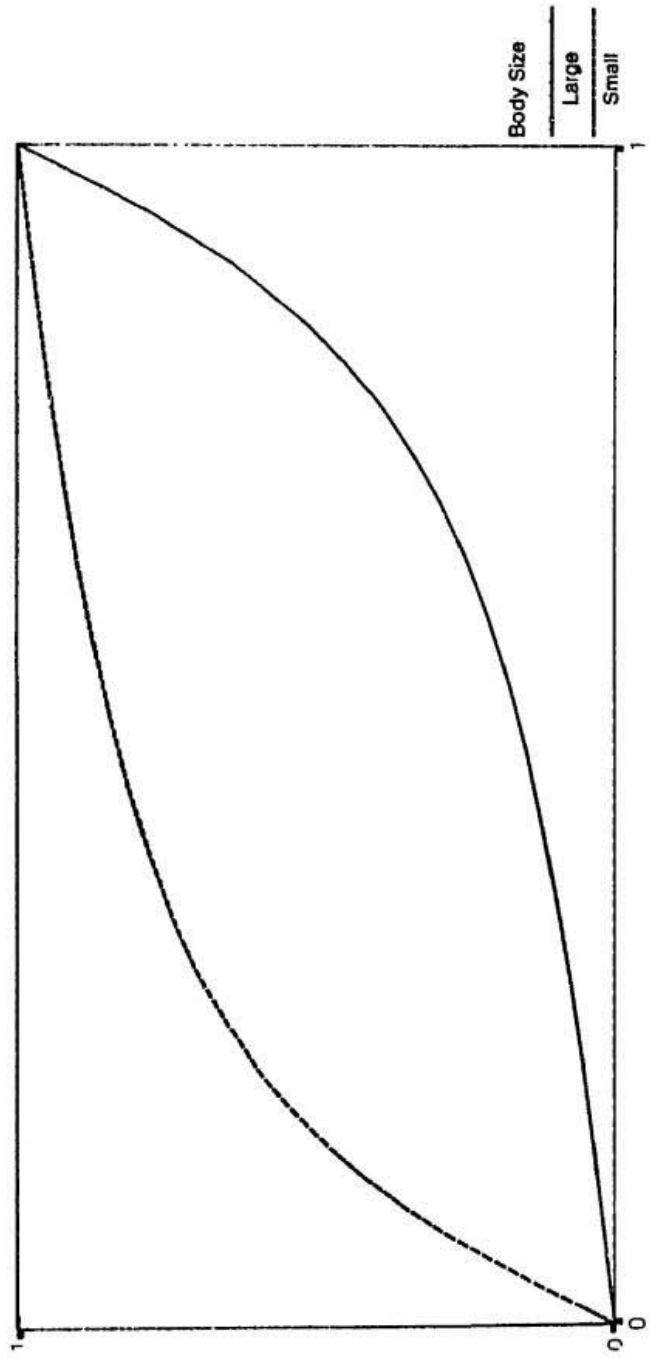

[1 - Survival Cost]
1.00
0.80
0.60
0.40
0.20
0.00
.10
.11
.12
.13
.14
.15
.16
.17
.18
.19
Effort

4.5.2 The Influence of Body Size on Reproductive Costs

Body size appears to influence the magnitude of reproductive costs within Freshwater and Watern Cove populations (the only populations for which 3 or more data points were available; Fig. 25). Although costs increase with effort at the highest expenditures of effort, the high costs associated with the smallest expenditures require explanation. These high costs for relatively low effort are incurred by the smallest females in each population.

If the survival cost to reproduction is influenced by maternal size and if there are large differences in size at maturity, then the cost "curve" within a single population may be a 3-dimensional function of cost, effort, and body size. Such a 3-dimensional surface would better reflect the differential costs for given expenditures of effort that are associated with different body sizes. Thus, cost curves for smallest and largest females within a population may be those represented in Fig. 27. The cost curve for small females is convex with respect to the abscissa whereas the cost curve for large females is concave. Thus, for low expenditures of effort, reproductive costs increase at faster rate for small females than they do for large females.

FIGURE 27. Hypothetical cost functions for two body sizes within a single population.


Body Size
Large
Small
1
0
0
1
Effort
Cost

4.5.3 The Physiological Basis for Reproductive Costs

The assumption that costs for a given effort increase as body size decreases has a physiological basis. Brook trout depend upon lipid reserves (comprising 4-6% total body weight) to meet the energetic demands imposed by low water temperatures and low food during winter (Cunjak, 1988). Cunjak and Power (1986) reported overwinter declines in lipid content of 28 and 29% in brook trout inhabiting the Koksoak River in northern Québec. These percentages are similar to the 30% reduction reported by Dutil (1986) for immature Arctic char in Nauyuk Lake, Northwest Territories.

The constraints imposed by metabolic allometry dictate that smaller individuals must allocate proportionately more energy to fat stores than larger individuals during periods of fasting and low food supply (Schmidt-Nielson, 1984; Dunbrack and Ramsay, unpubl.). The present study and that of Hunt (1969) confirm the prediction that smaller individuals are at a survival disadvantage during metabolically demanding periods. Smaller trout have lower overwinter survival probabilities than larger trout. Maturation further exacerbates this overwinter cost to survival. Eggs and sperm are largely comprised of lipids (Rowe et al., 1990). Thus, the preferential allocation of lipids to gonadal production and the loss of these lipids

during autumnal reproduction will further inhibit the ability of an individual to survive the winter. Therefore, a given allocation of body tissue to gonadal production should exact a greater cost from smaller individuals relative to larger individuals.

The physiological basis for this hypothesized cost mechanism for brook trout is similar to that reported by Clutton-Brock et al. (1982) in their long term study of the population biology of the red deer. Females bearing calves in a given year have reduced survival and calving probabilities the following year. Clutton-Brock et al. hypothesized that lactation depleted the fat reserves that red deer rely upon during the winter months when food abundance is low.

4.6 The Evolutionary Significance of Population Divergence in Brook Trout Life Histories

By comparing the populations having the most divergent life histories (Freshwater and Cripple Cove), I offer the following verbal model which describes the effects of growth rate on the covariation and evolution of life history traits in brook trout.

Population differences in individual growth are generated primarily by stream differences in food abundance (invertebrate biomass varied by a factor of 2.8 between

Cripple Cove and Freshwater rivers; cf. Table 3). Beyond the first year of life, Cripple Cove trout grow twice as fast as Freshwater trout (cf. Table 16). This reduction in growth rate increases the time it takes for Freshwater trout to attain the size at which maturation and reproduction are possible physiologically.

The fitness consequences of maturing at the physiologically minimum size depend on the benefits and costs of investing energy into present versus future reproduction. The benefits which arise from early reproduction are that an individual maximizes both the rate at which its genes are introduced into the population and its probability of surviving to reproduce. The costs which arise from reproducing at a small size are that an individual produces fewer offspring (since fecundity is positively correlated with size) and reduces its probability of surviving reproduction, and the winter, to reproduce in the future. Reduced growth in Freshwater females favours early maturity at a small size primarily because of the slow rate at which fecundity increases with age.

For maturation at a small size to be evolutionarily stable, Freshwater females must increase their age- and size-specific fecundity (cf. section 4.3.3). An additional pressure on reproductive investment for Freshwater females is the low food abundance which favours the production of large eggs. Relative to Cripple Cove females, Freshwater

females allocate 60% more body tissue to gonadal production. But the physiological constraints imposed by high reproductive investment, coupled with the metabolic constraints imposed by small body size during the winter, result in a 60% lower probability of surviving reproduction. The costs of reproduction associated with high reproductive effort are so great that Freshwater females are effectively semelparous individuals. The concave shape of the function which relates reproductive costs to reproductive effort can account for population divergence in age-specific expenditures of reproductive effort among the brook trout populations.

4.7 Summary

I have used a combination of field research, laboratory experiments, and empirically-based model simulations to test life history theory on populations of brook trout. The main results can be summarized as a rejoinder to the predictions specified in the Introduction and tested during the course of my research.

There is good evidence that population variation in brook trout life history can be adaptive on a small geographical scale. There are survival costs of reproduction in brook trout that increase with reproductive effort. The cost function appears to be concave upwards and

provides an empirical basis for theoretical cost functions that predict how semelparity and iteroparity can evolve within a species. Differences in size-specific reproductive effort, resulting from differences in food abundance, appear to effect differences in reproductive costs among populations. Reduced growth in brook trout favours maturation near the physiologically minimum size and high size-specific reproductive investment in egg size and egg number. Decreased food abundance favours the production of larger eggs at the cost of producing fewer eggs. Experimental manipulations, comparative field data, and model simulations support the prediction that maternal investment in offspring size and offspring number depends on the relationship between offspring size and survival and on the influence this relationship has on maternal fitness. The results also suggest that constant rather than variable investment in offspring size within and among broods will favoured in unpredictable, temporally heterogeneous environments.

Thus, the results provide direct and indirect evidence of how an environmental factor (food abundance) can effect both phenotypic and genotypic differentiation in life history traits on a small geographical scale. The life history strategies that emerge at the population level depend largely on the survival and fecundity consequences that differences in reproductive investment (through

physiological and development constraints) impose on individuals.

Chapter Five

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Appendix A. Randomizations of environments (1=high food, 2=low food) and egg size strategies (strategy VII (1=3.9 mm eggs, 2=4.7 mm eggs; strategy VIII [1=3.9 mm eggs, 2=4.3 mm eggs]; strategy IX [1=4.3 mm eggs, 2=4.7 mm eggs]) used in section 4.2.4.

Randomization	Environments	Strategies
1	1 1 1 1 1	1 2 1 1 2
2	2 2 1 2 1	1 2 2 1 1
3	2 1 2 1 1	2 2 2 1 2
4	2 1 2 2 2	2 1 1 2 1
5	1 2 2 2 2	1 2 1 1 2
6	2 1 2 2 1	1 2 1 2 2
7	2 2 1 1 2	1 1 2 1 2
8	1 2 1 2 2	1 2 1 1 1
9	2 2 1 2 1	1 1 1 1 1
10	1 2 2 2 2	2 2 2 1 2
11	2 2 2 2 1	2 2 1 2 1
12	2 1 1 2 1	2 2 1 1 1
13	2 1 2 1 1	2 2 2 2 2
14	1 1 2 1 2	1 1 2 1 1
15	2 1 1 2 1	1 1 1 1 1
16	2 1 1 2 2	2 1 2 1 1
17	1 1 2 2 1	1 2 2 1 1
18	2 1 2 2 1	1 1 2 2 2
19	2 1 1 2 1	1 2 1 1 1
20	1 1 1 2 1	1 2 1 2 2

Appendix B. Length (mean ± s.d.) of brook trout reared in the laboratory and fed ad libitum. First exogenous feeding of trout was in March, 1989. Fish were reared in water of ambient temperature and under light conditions of photoperiod 10 light: 14 dark. (Abbreviations: FW=Freshwater, CC=Cripple Cove, WC=Watern Cove; Sex - I=immature, M=male, F=female, C=combined mature and immature).

Population	Date	Sex	Length (mm)	n	Fecundity	Egg Size (mm)
FW	Aug 22	I	91.6 ± 15.7	9		
CC	"	I	92.0 ± 15.6	5		
WC	"	I	86.7 ± 13.0	18		
FW	Oct 23	I	127.0 ± 8.9	9		
CC	"	I	120.6 ± 18.2	5		
WC	"	I	108.6 ± 18.2	18		
FW	Dec 28	M	142.0 ± 8.9	3		
	"	F	122	1		
	"	C	133.1 ± 9.8	9		
CC	"	M	158	1		
	"	C	124.8 ± 22.9	5		
	"	M	138.0 ± 11.1	5		
	"	C	120.8 ± 21.2	18		
FW	Mar 14	M	140.0 ± 12.5	4		
	"	F	134.4 ± 8.1	5	165 ± 22	3.90 ± .30
	"	C	136.9 ± 10.0	9		
CC	"	M	135.0 ± 2.8	2		
	"	F	123.2 ± 14.2	2	101 ± 32	3.41 ± .32
	"	C	126.2 ± 8.9	5		

Appendix B (cont'd)

Population	Date	Sex	Length (mm)	n	Fecundity	Egg Size (mm)
WC	"	M	150.8 ± 11.2	5		
	"	F	122.6 ± 15.1	7	112 ± 28	3.65 ± .35
	"	C	124.5 ± 23.4	17		